DOCTORAL THESIS

The movement ecology of a breeding seabird

An investigation using accelerometry

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The movement ecology of a breeding seabird: An investigation using accelerometry

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ABSTRACT

Animal movement is a ubiquitous process and can have consequences ranging from an individual's energy expenditure to ecosystem dynamics. This study uses biologgers, primarily accelerometers, to record and examine the at-sea behaviours of black-legged kittiwakes (*Rissa tridactyla*) during their breeding period.

Accelerometers record the acceleration of an instrumented animal to give an indication of their behaviour and movements, yet their output can be particularly difficult to interpret. As such, this thesis begins with a method developed for the assignation of coarse-scale behaviours to accelerometry data. The method is a simple yet objective approach intended to be widely applicable. Using this method, we construct time-activity budgets for incubating and chick-rearing kittiwakes and apply activity-specific estimates of energy expenditure to these behaviours. We identify how kittiwakes allocate their time and what the energetic consequences of variation in time-allocation are. We present empirical evidence for chick-rearing kittiwakes expending more energy than incubating birds and identify that kittiwakes exhibit behavioural compensation whereby they limit energy expenditure across both foraging trips and days.

We also examine the flight behaviour of kittiwakes in relation to extrinsic conditions. We find that wind conditions do not seem to influence broader scale patterns in movements during foraging trips, however kittiwakes do display behavioural plasticity in response to wind conditions by optimising their flight speeds towards maximum range speeds. We also identify that to optimise flight speeds, kittiwakes change the strength at which they flap their wings, rather than the frequency.

Finally we present a serendipitous observation of predation of kittiwake chicks by a peregrine falcon. Although not directly related to movement ecology, this study documents novel predatory behaviour and highlights the importance of biological forces other than movement. Overall, the work presented in this thesis demonstrates that by examining the movement of individuals, it is possible to gain insights into various important aspects of their biology.

The research for this project was submitted for ethics consideration under the reference LSC 13/ 082 in the Department of Life Sciences and was approved under the procedures of the University of Roehampton's Ethics Committee on 14/03/2013

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To my examiners: Don't worry, I ramble on much less in the rest of this thesis.

Chapter 1

General introduction

Movement ecology

Movement is a ubiquitous process - nearly all organisms will change their spatial location at some stage in their life (Holyoak *et al.* 2008). From fine-scale reactionary movements to large-scale migrations, animal movement has consequences from instantaneous energy expenditure to ecosystem level dynamics, and is an intrinsic driving factor in the evolution and diversity of life (Nathan *et al.* 2008). Through morphological, physiological, and behavioural adaptations, animals have evolved to traverse their environments, and have spread into a vast number of niches and habitats in a great diversity of ways (Shine & Shetty 2001; Dial 2003a; b; Kawano & Blob 2013). To take a few examples from the vertebrata, fossorial mammals burrow through the earth, raptors soar with rising air currents, cetaceans migrate from polar to equatorial seas, and arboreal apes ascend into the jungle canopy; the diversity of movement adaptations present in nature enables animals to exploit resources across highly varied habitats.

With such a diversity of locomotory modes and wide-reaching implications, the study of animal movement has captivated researchers. Under the term movement ecology, research into this area has seen an upsurge in recent years, especially examining the movement of individual organisms (the Lagrangian approach) (Nathan *et al.* 2008). A search of Web of Science using the term “movement ecology” highlights this, showing a substantial increase in the number of publications under this topic, especially since 2008. It appears likely that this upwards trend will continue (Figure 1.1).

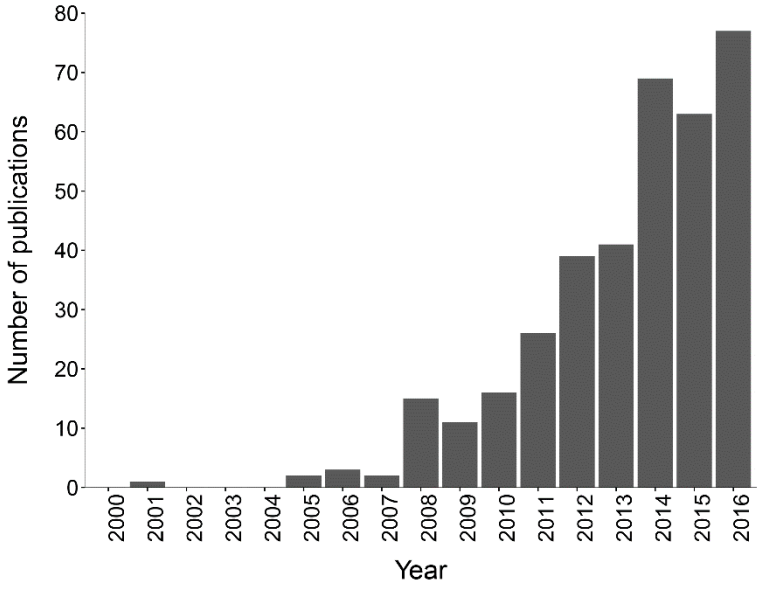

Figure 1.1 Number of publications per year as determined by a Web of Science search using the term "Movement ecology". The search was conducted in December 2016.

As with all biophysical processes (Brown *et al.* 2004), energy is central to animal movement. At the level of the individual, movement can account for a large proportion of daily energy expenditure (Brit-Friesen *et al.* 1989; Karasov 1992). Moving in a manner optimised towards judicious energy expenditure can therefore alleviate the total amount of energy individuals expend on movement. Indeed, there are myriad morphological, physiological and behavioural adaptations indicating that there is strong selection pressure on moving in a way that reduces energy expenditure. The fusiform shape of many aquatic animals, the thermal-seeking behaviour of soaring raptors and the hitchhiking behaviour of remoras are just a few of such adaptations.

Although traits that minimise energy expenditure tend to be selected for, energy expenditure is only one side of an individual's energy budget, with the other being energy gain. Energetic balance, (net energy gain – the difference between energy gain and energy

expended) is more important in determining an individual's success. Individuals able to minimise energy expenditure while maximising energy gain are more likely to have sufficient resources for reproduction, and be able to reduce the impacts of the costs of reproduction on future survival (Nisbet *et al.* 2000; Ellison 2003; Lescroël *et al.* 2009).

Movement is largely driven by the need to gather food, find mates, and avoid predation, while also being subject to variable environmental factors (Halsey 2016). Such factors result in animals having to make trade-offs against minimising energy expenditure during locomotion. For example, moving in a manner that minimises energy expenditure while fleeing a predator would likely result in death, thereby negating any minor gains from reducing energy expenditure. During foraging, movement is determined by potentially complex internal and external interlinking factors (Owen-Smith *et al.* 2010) that ultimately trade energy expenditure against potential energy gains. Optimal foraging theories predict that animals should move in a way that maximises net energy gain (Pyke *et al.* 1977), yet the complex suite of factors that can influence how animals move when foraging often leads to deviation away from optimal behaviours (e.g. Louzao *et al.* 2014; Foo *et al.* 2016). Although movement is a complex process determined by various influencing factors, through examining the movement of animals in-situ, it is possible to identify factors that can ultimately determine whether an animal is successful or not (Morales *et al.* 2010).

Measuring movement

Quantifying animal movement poses logistical challenges (Ropert-Coudert & Wilson 2005). This is especially true at the individual level, whereby continuously monitoring highly mobile or elusive animals can become unfeasible if not using a remote monitoring approach. Technological advances arising from the increasing demand for sophisticated consumer electronics have, however, resulted in biologging tools being widely available

and affordable for studying animal movement (Cooke *et al.* 2004). From capturing the extreme migration of arctic terns as they travel from breeding grounds in the Arctic to wintering grounds in the Antarctic (Egevang *et al.* 2010), to tracking in fine detail the movements of plankton using nanotechnologies (Lard *et al.* 2010), the application of technology to animal tracking has proven revolutionary across the full spectrum of animal movement. Animal-borne biologgers in particular have been pivotal in enhancing our understanding of animal movement (Wilmers *et al.* 2015); according to some we are living in "a golden age of animal movement" (Wilmers *et al.* 2015; Hays *et al.* 2016). By facilitating the tracking of individuals for extended periods of time regardless of scale of movement and location, biologging tools enable us to examine the consequences of movement at the individual level and allow interrogation of animal movement under theories of movement ecology and energy optimisation.

As with any research tool, biologgers have considerations and limitations for their use. One major consideration when using biologgers is device effects: the effect that carrying the device has on the instrumented animal, both in terms of the welfare of the animal, as well as the influence this has on the data being collected (White *et al.* 2013). Device effects can vary greatly in severity and duration, potentially spanning behaviour (e.g. Kidawa *et al.* 2011; Chivers *et al.* 2016), physiology (e.g. Ludynia *et al.* 2012), reproduction (e.g. Beaulieu *et al.* 2010) and survival (e.g. Thaxter *et al.* 2016). Causes of device effects can be complex, with factors such as shape (Vandenabeele *et al.* 2015), positioning (Vandenabeele *et al.* 2012, 2014), duration of deployment (Wilson & McMahon 2006), and method of device attachment (Thaxter *et al.* 2016) (including whether the device is implanted or attached externally (White *et al.* 2013)), all being potential contributors to negative outcomes. Handling effects and other sources of researcher disturbance can also have deleterious impacts on instrumented animals, yet are often overlooked (Carey 2011; Thomson &

Heithaus 2014). Despite these effects, biologgers are often the only feasible way to collect movement data from individual free-ranging animals. Ultimately the use of biologgers is a trade-off between the potential impacts on the instrumented animals, and the importance of the research questions being asked, however this is a subjective judgement involving stakeholders with often differing views (Wilson & McMahon 2006). Regardless of opinion as to what is an acceptable burden to impose on an animal, reducing the impacts of biologgers is favourable for all interested parties, and the continuing miniaturisation of devices coupled with a greater understanding of device effects will hopefully contribute to achieving this.

Another important consideration when using biologgers is how to manage and analyse the data they generate. With biologging entering the realm of big data (Kays *et al.* 2015), the associated challenges of developing the tools necessary to manage and interpret the data have arisen. The number of parameters currently measured by biologgers is relatively small (Payne *et al.* 2014), mainly including location, acceleration, barometric pressure (depth/altitude) and temperature. However, each parameter poses its own distinct challenges in terms of analysis, which is further compounded by the broad questions the data can potentially answer. In combination this has resulted in the methods used to analyse biologging data being highly variable, spanning visual interpretation of datasets (e.g. Hassrick *et al.* 2007) to complex machine-learning type analyses (e.g. Guilford *et al.* 2009). With biologgers offering an objective tool for quantifying behaviour, introducing bias through visual interpretation can undermine their value, whereas computationally complex approaches may be beyond the grasp of many researchers, and the outputs of such approaches can be difficult to interpret with respect to the behaviour of the instrumented animal.

Accelerometry

Accelerometers are biologgers that typify the problem of managing and interpreting biologging data; by recording at potentially high temporal resolution (from 0.5Hz to 10,000Hz) they are perhaps the biologging device that currently has the potential to generate the most data per unit of time (battery life permitting). Accelerometers record acceleration of an organism's mass due to the movement of its body parts (Halsey *et al.* 2011). Their use in studies of physical activities in humans has long been established (Saunders *et al.* 1953; Yang & Hsu 2010), however their application to free-ranging animals was a much later development (Yoda *et al.* 2001; Shepard *et al.* 2008).

Accelerometers measure acceleration across one, two, or three axes, with tri-axial accelerometers being the most widely used in studies on free-ranging animals. By measuring over more than one axis it is possible to derive the orientation of the logger, and in turn the orientation, or posture, of the instrumented animal (Tsuda *et al.* 2006; Halsey & White 2010; McClune *et al.* 2014) (Figure 1.2). To identify orientation of the animal, recorded acceleration data are averaged over a time period. By subtracting this value from the raw acceleration values, it is possible to get a measurement of the dynamic movement of the animal (Gleiss *et al.* 2011) (Figure 1.2). With the static component of acceleration data indicating posture and the dynamic component of the data indicating movement, accelerometers have been successfully adopted, and indeed are regularly used, to identify behaviours and activity levels of instrumented animals (e.g. Shepard *et al.* 2008; Halsey *et al.* 2009, 2013; Halsey & White 2010; McClune *et al.* 2014).

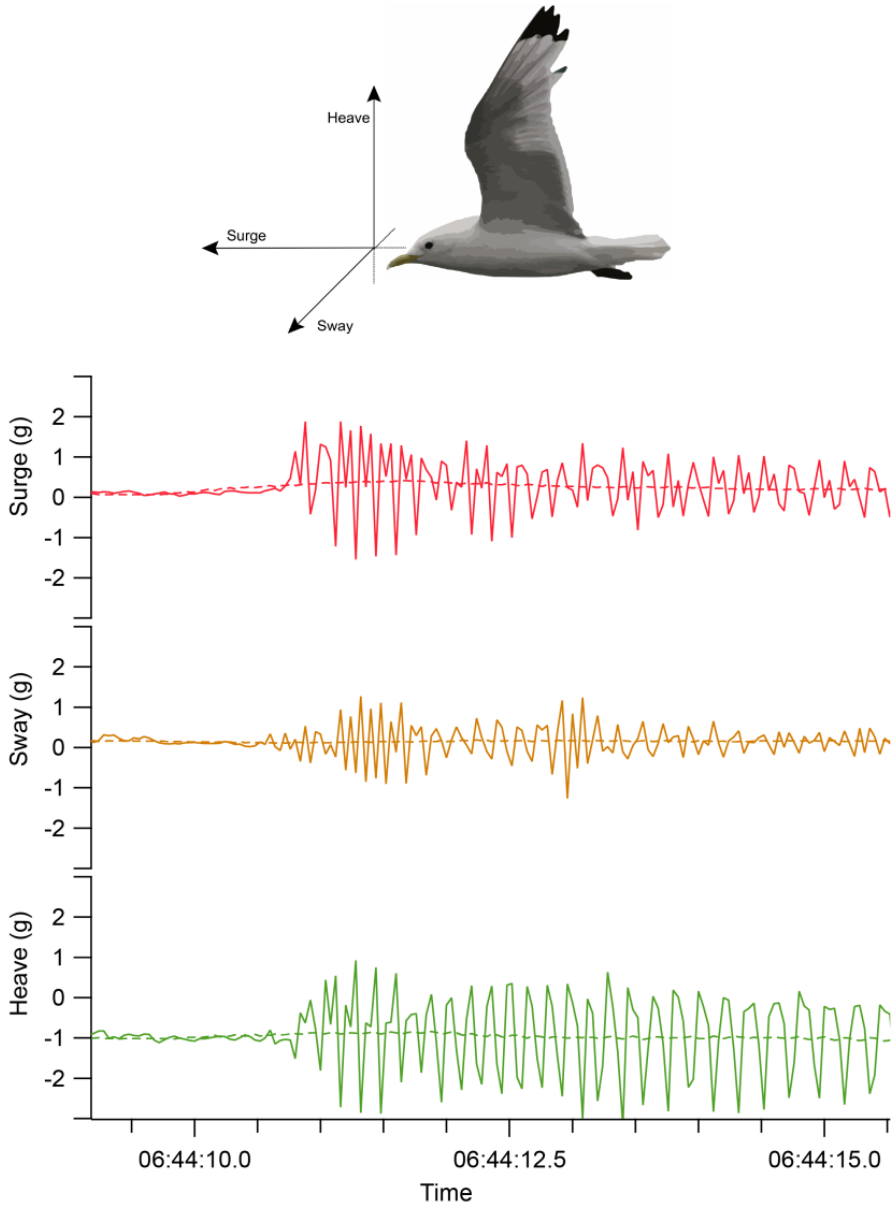

Figure 1.2 The three channels recorded on a tri-axial accelerometer in relation to the instrumented animal (top). The graph shows the acceleration values recorded by each of these three axes during a period when a bird transitioned from resting to continuous flight. The more variable signal from each axis represents raw acceleration value, while the dotted lines show the smoothed component of the acceleration signal, otherwise known as the static acceleration. By taking a measure of the difference between the static acceleration values and the raw acceleration values, a metric of the dynamic movement of the instrumented animal can be derived.

An objective of many studies employing accelerometry is to quantify energy expenditure (e.g. Murchie et al. 2011; Payne et al. 2011; Enstipp et al. 2011; Elliott et al. 2013b; Nie et al. 2015). Two approaches tend to be used for this purpose: applying activity-specific estimates to time-activity budgets (e.g. Shamoun-Baranes *et al.* 2012), or applying estimates of energy expenditure to measures of dynamic body acceleration (e.g. Elliott *et al.* 2013b). Applying activity-specific estimates of energy expenditure to accelerometry derived time-activity budgets essentially updates the more established approach of constructing time-energy budgets from observational data. By using behavioural information derived from accelerometry data, this updated approach has the benefit of being based on objective, continuous, high resolution behavioural data. By applying calibration values of energy expenditure to measures of dynamic body acceleration, continuous estimates of energy expenditure that take into account the total amount of movement of the individual can be derived. A number of studies have employed this approach for estimating in-situ energy expenditure, revealing some fascinating insights into how animals allocate their energy (Elliott *et al.* 2013b; Williams *et al.* 2014). Such estimates can only be as robust as the values they are calibrated with however, so where possible an effort should be made to quantify the error associated with these measures. Nevertheless, through accelerometry, high resolution estimates of in-situ energy expenditure are now a possibility.

Aside from the more obvious direct measures of movements, novel multi-disciplinary questions, such as interactions with the environment under changing conditions, are now being addressed using accelerometry (Payne *et al.* 2014). The high temporal resolution of data collected by accelerometers is also being exploited to identify more detailed information regarding animal movement and maximise the amount of information it is possible to derive from such datasets. For example, it is possible to identify prey acquisition

in large seabirds due to changes in their wingbeat stroke frequency (Sato *et al.* 2008). It is also possible to identify extremely short-lived behaviours including escape responses (Broell *et al.* 2013), or the moment a predator pounces on its prey (Williams *et al.* 2014). By combining accelerometers with other biologging devices such as GPS and cameras, an even greater range of research questions can be addressed, allowing quantification of biological features such as prey capture events (Watanabe & Takahashi 2013) or adjustments of flight effort in response to wind conditions (Kogure *et al.* 2016; Weimerskirch *et al.* 2016).

A potential barrier to the use of accelerometers is the perceived difficulty in analysing their output. This is exacerbated by the broad suite of approaches available to analyse acceleration data, and little consistency or repeated use of methods in the literature. Identifying and assigning behaviours is often one of the first steps in interpreting acceleration data. Methods available for doing this can range from visual interrogation of the shape of the data (e.g. Gómez Laich *et al.* 2009) to the use of more computationally complex machine-learning type approaches (e.g. Gerencsér *et al.* 2013). This varying suite of approaches potentially may make comparisons of behavioural data derived from accelerometers across studies inappropriate. As such there is a requirement for a straightforward, standardised method or protocol applicable to studies identifying and assigning behaviours to accelerometry data.

Seabirds

Seabirds are a group for which biologging studies have provided, and continue to provide, a real opportunity to gain insights into otherwise unknown behaviours (Burger & Shaffer 2008). By breeding on land yet feeding often far out at sea, seabirds are out of the practical reach of researchers for much of their lives. To continuously monitor the behaviour of individual seabirds, especially when at sea, a biologging approach is by far the most

practical current option (Burger & Shaffer 2008). This is in part highlighted by the fact that, when considering total number of biologging studies, seabirds are the most investigated group in comparison to other diving animals. However this is also likely to be due to there being a greater number of species of seabirds than other diving animals (Ropert-Coudert *et al.* 2010).

As a group, seabirds are typified by a number of broad life-history traits, including: long lifespans, deferred maturation, small clutch sizes and extended chick-rearing periods (Schreiber & Burger 2002). Although they share these common traits, seabirds are a diverse group of species. Their diversity is perhaps best highlighted in their locomotory behaviour. For example, penguins are amongst the heaviest of birds, are flightless and are capable of diving to great depths (Sato *et al.* 2002), while albatrosses, which are by no means light, have mastered flight to soar great distances while expending little energy (Weimerskirch *et al.* 2000). Between these two extremes of locomotory styles other species display intermediary styles, for example, auks are capable of flight and can dive to great depths (Elliott *et al.* 2013a), gannets can fly great distances but have also adapted to plunge dive in order to reach prey beyond the surface waters (Ropert-Coudert *et al.* 2003), and storm petrels exhibit a flap-glide flight style which they interrupt to pick food from the sea surface (Obst *et al.* 1987).

During the breeding period seabirds are central place foragers; they are limited in their foraging ranges by the need to return to their breeding sites for mating, incubation or chick-rearing. This constraint on time available for individuals to spend away from their nest has implications for how they behave throughout and between the varying stages of this period (Shaffer *et al.* 2003). The combination of being constrained through central place foraging, needing to meet the energetic demands of raising young, and needing to

balance investment in offspring with self-maintenance, provides a complex yet compelling set of conditions in which to study movement ecology.

Behavioural strategies shaped by central place foraging constraints have been described through the use of biologgers. For example, in many species a dual foraging tactic has been recorded whereby individuals embark on longer foraging trips, during which it is posited that they obtain food for self-maintenance while they carry out shorter feeding trips to capture food for their young (Granadeiro *et al.* 1998; Welcker *et al.* 2009b). Furthermore, despite incurring commuting costs, individuals are consistently recorded foraging away from their colony. Such behaviour is potentially a tactic for increasing foraging efficiency through reduced intraspecific competition (Davoren *et al.* 2003) or to avoid areas that may already have been prey depleted in the waters surrounding the colony (Ballance *et al.* 2009; Elliott *et al.* 2009). A vast majority of such studies examine the spatial distributions of foraging seabirds and it is often the case that time spent in different behaviours is not explicitly considered. By quantifying behaviour, such strategies could be considered with a more robust indication of energy expenditure, resulting in a more detailed understanding of the drivers of the movement ecology of foraging seabirds. Indeed, there is already evidence of the importance of considering energetic expenditure along seabird foraging trips, as this measure has been suggested to limit the population sizes of seabird colonies (Ballance *et al.* 2009).

Understanding the movement ecology of seabirds could be considered especially important given their current status. With 346 known species, seabirds are highly threatened and declining at a substantial rate in comparison to other groups of birds with similar numbers of species (Croxall *et al.* 2012). Changes in population sizes vary vastly between species and regions, however it has been estimated that species for which there is sufficient monitoring

data declined by 69.7% between 1950 and 2010 (Paleczny *et al.* 2015). Through gaining a more in-depth understanding of the influencing factors and the consequences of the movement of seabirds when away from the land, not only would potential mechanisms leading to their declines (such as shifting distributions of prey (e.g. Crawford *et al.* 2008)) be uncovered, but we'd also be able to more sufficiently predict how they would respond to changing conditions.

The kittiwake

This thesis focuses on the movement ecology of the black-legged kittiwake (*Rissa tridactyla*) (hereafter kittiwake), a widely distributed gull species inhabiting the northern hemisphere. Kittiwakes differ from most other gull species in that they nest predominantly on the ledges of sea-cliffs (Cullen 1957). As with most seabirds they tend to reproduce annually (Schreiber & Burger 2002), with the breeding season corresponding with late spring to summer across their range.

The locomotory behaviour of kittiwakes makes them particularly well-suited to studies of movement ecology. When flying, kittiwakes employ a flap-glide style of flight, with the vast majority of time spent flapping. This almost continuous flapping style of flight provides a measurable indication of the amount of effort birds are exerting when flying (Pennycuick 2008). Furthermore, flight is their only mode of locomotion; kittiwakes are incapable of actively pursuing prey through the water column and as such they feed at, or near, the sea surface (Coulson 2011). This means that any spatial movements they make in order to locate prey occur through increasing either their foraging range or the amount of time they dedicate to foraging (Kotzerka *et al.* 2009). The movement of kittiwakes can therefore largely be considered in terms of latitude and longitude (i.e. 2 dimensions) as opposed to

diving birds, for which depth becomes a necessary consideration (3 dimensions) (Grémillet *et al.* 1999).

Being confined to feeding at the sea-surface also makes kittiwakes particularly vulnerable to changes in food availability. Kittiwakes feed mainly on near-surface schooling fish (sand-eels or clupeids mostly) and both short-term and long-term fluctuations in prey availability have been demonstrated to greatly impact their condition and reproductive success (Suryan *et al.* 2002; Frederiksen *et al.* 2005). Such changes in prey availability have been linked to shifts in water temperature (Frederiksen *et al.* 2007; Hatch 2013; Sandvik *et al.* 2014; Carroll *et al.* 2015) and depletion due to fisheries (Furness & Tasker 2000; Frederiksen *et al.* 2004). Perhaps as a result of their sensitivity to changing conditions, along with previously elevated population sizes due to fishery discards (Coulson 2011), kittiwakes are declining in numbers across their range. In the UK, numbers of breeding pairs have declined by 44% since 2000 (JNCC 2016). This decline in numbers is also accompanied by a decline in productivity at a rate of 0.02 chicks per nest per year (JNCC 2016). If the trend in population decline continues, kittiwakes will decline by a further 35% over 25 years (Cook & Robinson 2010). With such a decline in numbers, seemingly driven by changes away from the land, it is increasingly important to understand what individuals are actually doing when out at sea.

A number of studies have employed biologging tools to examine the at-sea movements of breeding kittiwakes (e.g. Kotzerka *et al.* 2009; Chivers *et al.* 2012; Soanes *et al.* 2013; Elliott *et al.* 2014; Heggøy *et al.* 2015). The majority of these studies examine spatial distributions of foraging kittiwakes. Although such studies are beneficial for identifying potential responses of kittiwakes to the conditions they face, or for identifying important feeding areas, they tend to lack detailed information regarding how they are allocating their time

to behaviours. Such information is potentially more pertinent to understanding how individuals function in their environment as it has a direct link to energy expenditure. Furthermore, as with many studies identifying the at-sea movements of seabirds, the response of kittiwakes to varying extrinsic conditions such as wind speed and direction has often been overlooked. A substantial influence of wind conditions on the movements of seabird species such as the albatrosses has been described (e.g. Weimerskirch *et al.* 2000, 2012), however kittiwakes employ a drastically different flight style to albatrosses and are therefore not likely to respond to wind in the same way. Nevertheless, wind is likely to play an important role in shaping movement patterns and energetics of kittiwakes when at-sea (Spear & Ainley 1992). It is therefore necessary to bridge this knowledge gap, not only to develop a more complete idea of how kittiwakes function in their environment, but also to gain a more comprehensive understanding of how differences in morphology and behaviour shape the movement of such animals in response to extrinsic factors.

The energy expenditure of kittiwakes during the breeding period has been calculated in numerous studies (Gabrielsen *et al.* 1987; Thomson *et al.* 1998; Golet *et al.* 2000; Jodice *et al.* 2002, 2003, Welcker *et al.* 2009a, 2014; Schultner *et al.* 2010). Notably such work has detailed variations in energy expenditure within and between populations, as well as the importance of time spent away from the colony in influencing daily energy expenditure. In addition, kittiwakes have been reported operating at an intrinsic energy ceiling, whereby individuals apparently had a limit to the amount of energy they expend per day (Welcker *et al.* 2010). To estimate the energy expenditure of kittiwakes in all of these studies, the doubly labelled water approach was used. This method has a low temporal resolution, giving total values of energy expenditure over days. As such, although these studies have highlighted interesting considerations of the energetic expenditure of kittiwakes, they have not been able to examine energy expenditure in detail and directly link the movements

these birds make throughout the day to the amount of energy they expend. As findings indicate the importance of at-sea activity and a potential need for judicial energy expenditure for kittiwakes, there is a clear need for studies examining the at-sea behaviour and energetics of kittiwakes in greater detail.

Study sites

Puffin Island, Wales

A large proportion of the work presented in this thesis relates to primary data collected between May and August in both 2013 and 2014 on Puffin Island (53°19'05"N, 04°01'40"W). Situated 600 m off the coast off Anglesey, North Wales, Puffin Island hosts approximately 385 breeding pairs of kittiwakes (Natural Resources Wales, unpublished data) as well as numerous other seabird species. The kittiwake colony is comparable to the size of kittiwake colonies around the UK, which range in size from a few pairs to over 100,000 pairs (Coulson 2011). As Puffin Island is located in North Wales, the birds breeding here are limited to foraging in the relatively shallow surrounding waters of the Irish Sea. Ringing of seabirds has taken place over the last 30 years by a local ringing group (the SCAN ringing group), however the use of Puffin Island as a more intensive site for seabird research is a recent development.

Middleton Island, Alaska

Work is also presented based on a dataset collected by Dr Kyle Elliott, analysed and interpreted here for the first time, which concerns kittiwakes breeding on Middleton Island, Alaska (59°26'59"N, 146°18'26"W). These data were collected between May and June 2013. Situated 120 km from land, at the edge of the continental shelf, Middleton Island differs widely in both environmental and human factors when compared to Puffin Island. Kittiwakes breeding there have access to both the shallow waters of the continental

shelf as well as the deeper oceanic waters beyond (Hatch 2013). As the island used to be a US Air Force facility, there are a number of abandoned buildings. These structures have provided suitable nesting sites for kittiwakes and in turn they offer a convenient platform from which to study these birds. With approximately 12,000 breeding adults, a far greater number of kittiwakes inhabit Middleton Island in comparison to Puffin Island.

Aims and scope

The overarching aim of this thesis is to use accelerometry to reveal and explain patterns in the movement ecology of a breeding seabird. In particular we focus on measuring at-sea behaviours in light of potential energetic consequences. Although the study focuses on kittiwakes, it is intended that the findings presented can be considered in a broader context. It may be that the findings we present can apply directly to other species, or perhaps they are in stark contrast with others and present talking points from which further hypotheses can be generated. The chapters are stand-alone and tied by the common link of the movement ecology of kittiwakes, bar chapter 5 which is a serendipitous study of kittiwake chick predation and highlights the fact that other biotic factors can supersede the influences of movement behaviour and energy economies on breeding success.

Thesis outline

Chapter 2

Interpreting behaviours from accelerometry: a method combining simplicity and objectivity

This study provides a methodological approach for assigning coarse-scale behaviours to accelerometry data. Objective identification of behaviours in accelerometry data is

generally lacking, and this chapter proposes a simple, validated approach that can be applied to kittiwakes as well as other species.

Collins, P.M., Green, J.A., Warwick-Evans, V., Dodd, S., Shaw, P.J.A., Arnould, J.P.Y. & Halsey, L.G. (2015) Interpreting behaviors from accelerometry: a method combining simplicity and objectivity. *Ecology and Evolution*, **5**, 4642–4654.

Chapter 3

Energetic consequences of time-activity budgets for a breeding seabird

The research presented in this chapter uses the method presented and validated in chapter 2 to construct time-activity budgets for breeding kittiwakes. The resultant time-activity budgets are combined with published values of activity-specific metabolic costs to estimate the energy expenditure of free-ranging kittiwakes during the incubation and chick-rearing stages of the breeding period. The energetic consequences of variation in time allocation to behaviours are examined.

Collins, P.M., Halsey, L.G., Arnould, J.P.Y., Shaw, P.J.A., Dodd, S. & Green, J.A. (2016) Energetic consequences of time-activity budgets for a breeding seabird. *Journal of Zoology*, **300**, 153–162.

Chapter 4

The journey, not the destination: How windscapes influence the flight behaviour of a breeding seabird

Using the method presented in chapter 2, and building on the findings from chapter 3, this study employs accelerometry data in combination with GPS and wind data to examine in detail the flight behaviour of kittiwakes. In particular this study focuses on the influence of

wind, examining its influence on the timing, course and speeds of flights. Attention is also paid to the wingbeat patterns of kittiwakes when in flight, identifying how flapping speed and strength change when flying at different speeds.

Collins, P.M., Green, J.A., Elliott, K.H., J.P.Y., Shaw, P.J.A. & Halsey, L.G., J.P.Y. The journey, not the destination: How windscapes influence the flight behaviour of a breeding seabird. In preparation.

Chapter 5

Predation of Black-legged Kittiwakes, Rissa tridactyla, by a Peregrine Falcon Falco peregrinus: insights from time-lapse cameras

This short communication details the predation of kittiwake chicks by a peregrine falcon (*Falco peregrinus*) as recorded by time lapse cameras. The paper describes both the possibility of using remote cameras to determine nest fate in cliff-breeding seabirds as well as the previously undocumented behaviour of the peregrine falcon predating kittiwake chicks during periods of low light.

Although not directly related to the movement ecology of kittiwakes, the images forming the basis of this study were captured as part of the fieldwork on Puffin Island during which the data for chapters 2 and 3 were collected. Indeed, were it not for the peregrine's actions leading to the breeding failure of many of the study birds breeding on Puffin Island during the 2013 and 2014 field seasons, this thesis was likely to have ended up being very different in scope.

Collins, P.M., Green, J.A., Dodd, S., Shaw, P.J.A. & Halsey, L.G. (2014) Predation of Black-legged Kittiwake chicks *Rissa tridactyla* by a Peregrine Falcon *Falco peregrinus* : Insights

from time-lapse cameras. *The Wilson Journal of Ornithology*, **126**, 158–161.

Chapter 6

Discussion

This chapter summarises and ties together the findings of this thesis in light of the over-arching aim of using accelerometry to investigate the movement ecology of a breeding seabird. Research is considered in terms of the wide implications of findings, as well as species-specific considerations relating to the black-legged kittiwake. Ideas for further research are also detailed.

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Chapter 2

Interpreting behaviours from accelerometry: a method combining simplicity and objectivity

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Abstract

Quantifying the behaviour of motile, free-ranging animals is difficult. The accelerometry technique offers a method for recording behaviours but interpretation of the data is not straightforward. To date, analysis of such data has either involved subjective, study-specific assignments of behaviour to acceleration data or the use of complex analyses based on machine learning. Here we present a method for automatically classifying acceleration data to represent discrete, coarse-scale behaviours. The method centres on examining the shape of histograms of basic metrics readily derived from acceleration data to objectively determine threshold values by which to separate behaviours. Through application of this method to data collected on two distinct species with greatly differing behavioural repertoires, kittiwakes and humans, the accuracy of this approach is demonstrated to be very high, comparable to that reported for other automated approaches already published. The method presented offers an alternative to existing methods as it uses biologically-grounded arguments to distinguish behaviours, it is objective in determining values by which to separate these behaviours, and it is simple to implement, thus making it potentially widely applicable. The R script coding the method is provided.

Introduction

Behaviour is a manifestation of movement and can account for a large proportion of energy expenditure (Karasov 1992; Rezende *et al.* 2006), thus allocation of time to different behaviours can greatly affect an individual's survival and reproduction (Nagy *et al.* 1999). Behaviour can be quantified over a range of biological scales, from within individual changes over short time-scales (e.g. changes in behaviour whilst foraging (Ropert-Coudert *et al.* 2004)), to persistent changes in group behaviour over time (e.g. changes in time-spent foraging in response to increased inter-specific competition (Namgail *et al.* 2006)). Yet, despite its importance, collecting sufficiently accurate, quantitative data on behaviour for free-ranging animals tends to be problematic, especially in motile and/or elusive species (Ropert-Coudert & Wilson 2005). To address this, a range of biotelemetry approaches have been, and continue to be, developed to monitor animals remotely (Cooke *et al.* 2004). The most widely used biotelemetry devices collect positional data, and such devices have provided invaluable insights into species distributions across a range of spatial and temporal scales (Cagnacci *et al.* 2010). However, to elucidate behaviour from such positional data alone is complex, typically involving either making assumptions (Freeman et al., 2010), introducing statistically complex behaviour assignments (Guilford *et al.* 2009; Cristescu *et al.* 2014), or coupling the data with those obtained from other devices (Dean *et al.* 2013).

Among these other devices, the use of accelerometers to identify behaviours in free-ranging animals has become increasingly common in recent years (Yoda *et al.* 2001; Tsuda *et al.* 2006; Halsey & White 2010; Zimmer *et al.* 2011; Williams *et al.* 2014). Accelerometers measure the acceleration of an organism across one, two or three axes. By measuring across multiple axes, it is possible to derive the orientation of the logger which, in relation to gravitational force, in turn makes it possible to derive the orientation of the

instrumented animal (Tsuda *et al.* 2006; Halsey & White 2010; McClune *et al.* 2014) . The moment-to-moment difference between the acceleration recorded by the logger and the orientation of the logger indicates the dynamic movement of the animal's centre of mass (Gleiss *et al.* 2011). Accelerometers confer the advantage over direct observations and inference from other biologging tools, such as GPS loggers, of being able to record at high temporal resolutions (from 0.5 to 10,000Hz), allowing measurement of short-lived behaviours such as escape responses or feeding events (Kawabata *et al.* 2014; Carroll *et al.* 2014) as well as continuous measurement of coarse-scale behaviours such as flight, resting, swimming and running (Shepard *et al.* 2008; Halsey *et al.* 2009; McClune *et al.* 2014).

However identifying discrete behaviours in accelerometry data at all temporal scales has to date largely involved subjective assessments of data or, as with identifying behaviour from positional data, the use of complex computational techniques; both of which often lack validation (Bidder *et al.* 2014). This lack of consistency has resulted in numerous techniques being developed for classification of such data. The simpler methods available in the literature tend to be reliant on separating behaviours by specific threshold values of metrics derived from acceleration data. These are typically determined through comparison with a source of validation such as video recorded images (Kawabata *et al.* 2014), or through subjective inspection of the data (Gómez Laich *et al.* 2009); in both cases such approaches are, therefore, largely study-specific and potentially labour intensive. Furthermore, despite their efficacy, objectivity and increasing availability in statistical software packages (Nathan *et al.* 2012; Gerencsér *et al.* 2013; Campbell *et al.* 2013; Bidder *et al.* 2014; Carroll *et al.* 2014), approaches based on machine learning, which are also reliant on a source of validation and comprise numerous types of analyses, are conceptually difficult and therefore potentially inaccessible to many biologists. Indeed, such complexities may discourage the collection and use of accelerometry data. A

computationally simple method for interpreting behaviours from accelerometry data, which is not inherently reliant on a source of validation yet which also incorporates objectivity, is currently lacking. A key consideration which emerges when evaluating and choosing methods to interpret such data is the level of information required to answer the target research questions. In many studies this might mean that just the coarse-scale behaviours need to be identified; for example, when comparing time-activity budgets between individuals or groups (Gómez Laich *et al.* 2011; Le Vaillant *et al.* 2012) or for isolating certain behaviours to calculate associated energetic costs (Wilson *et al.* 2006). Even for studies identifying finer-scale behaviours and short lived events such as characteristics of limb-movement during locomotion, identifying the coarse-scale behaviours is often a necessary first step in analysis (Kawabata *et al.* 2014).

This study presents a computationally simple method for assigning coarse-scale behaviours to accelerometry data. Discrete behaviours are assigned by using objectively identified separation points in frequency histograms of simply-calculated metrics derived from accelerometry data. Behavioural assignments using this method are presented and independently validated for two distinct species with disparate modes of locomotion: black legged kittiwakes *Rissa tridactyla* and humans *Homo sapiens*.

Materials and methods

Data collection

Tri-axial accelerometers (X8m-3 Gulf Coast Data Concepts, LLC; recording range ±8 *g*, resolution: 0.001 *g*, weight: 14 g), set to record at 25 Hz, were attached to feathers on the centre of the backs of seven kittiwakes using clothed black Tesa® tape. The placement of the accelerometer was kept as consistent as possible across all birds. In addition to the accelerometers, birds were deployed with salt water immersion loggers (GLS Mk18-H

British Antarctic Survey, weight: 1.9 g) on the tarsus via cable tie attachment to existing metal leg rings. These loggers record a value between 0 and 200 once every ten minutes, measuring the proportion of time the logger was immersed in salt water over the previous epoch. Average body mass was 357 ± 20 g (mean ±SD) and data loggers weighed on average 4.5 ± 0.2% of body mass, which is within recommendations for deployment weight (Bridge *et al.* 2011). All seven birds were recaptured but one of the salt water immersion loggers was not functioning upon removal, giving a final sample size of six combined deployments. Deployment time ranged from 47 – 74 h during which time birds exhibited normal breeding behaviour, including incubation of eggs, rearing of chicks (dependent on which breeding stage they were at) or absence from the nest (most likely on foraging trips). Fieldwork was carried out on Puffin Island, North Wales (53° 19' 05" N, 04 °01 '40" W) in July 2013. All work was carried out under Countryside Council for Wales permit number (44043:OTH:SB:2013).

The same tri-axial accelerometers set to record at 25 Hz (n=5) or 40 Hz (n=1) were attached to the sternum in a vertical orientation using Tesa® tape on six humans. Participants were instructed to undertake three activities for approximately five minutes each: sitting, walking and running. All participants carried out each of the activities once and in the same order. Duration of deployment ranged from 14 – 28 mins.

Approach

The method of behavioural assignment presented here consists of a step-wise process which assigns pre-determined behaviours to acceleration data by using objectively identified threshold values of metrics derived from raw acceleration data (outlined in Figure 1). Initially, behaviours to be classified were considered and metrics thought likely to differ depending on these behaviours were calculated from raw accelerometry data.

Histograms of these metrics were then plotted to identify any patterns potentially indicative of discrete behaviours. These histograms, coupled with knowledge of the target species and the target behaviours, were then used to select the metrics most suitable for assigning behaviours from the accelerometry recordings. Behaviours were assigned dependent upon threshold values of these metrics. These thresholds were objectively determined values relating to the shape of the histograms, specifically the minimum frequency of data points falling between peaks (the inter-peak frequency minimum).

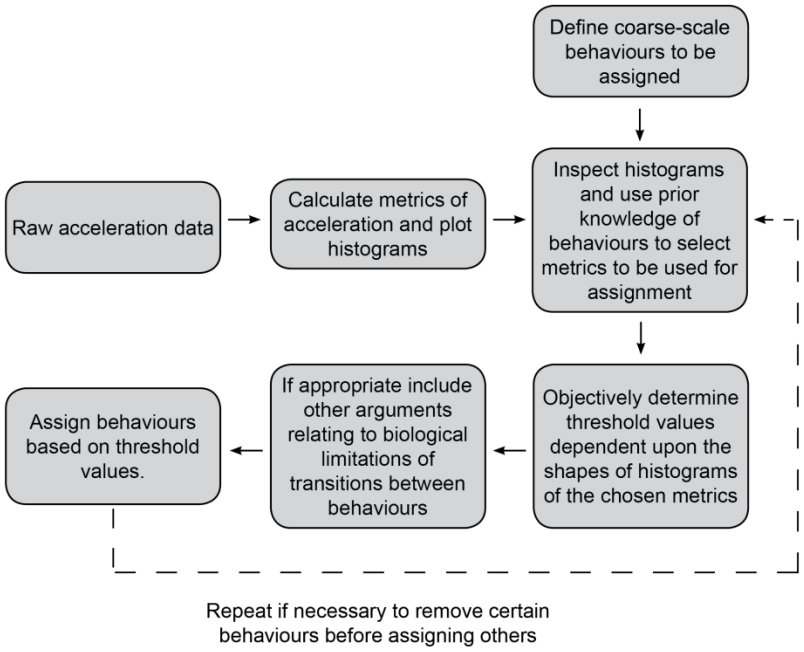

Figure 2.1. Flowchart of the process developed for assigning behaviours to accelerometry data.

Calculating metrics of acceleration

To identify metrics potentially indicative of discrete behaviours in both kittiwakes and humans, the following 10 metrics were calculated to 1-second intervals across the dataset of each subject bird or participant: mean acceleration and standard deviation of raw acceleration for each of the three axes (heave, surge and sway), pitch of the body, and roll

of the body; overall dynamic body acceleration (ODBA); and vectorial dynamic body acceleration (VeDBA). Mean and standard deviation of the acceleration values were calculated over a moving period of 25 data points (representing a duration of one second). Pitch (the angle of the device and therefore also of the bird or participant) and roll (the side to side movement of the bird or participant) were derived from all three axes using the following equations:

Pitch=Arctan $(X / (Y^2 + Z^2)^{½})$ ** (180/pi)*

Roll = Arctan $(Y/ (X^2 + Z^2)^{1/2})$ ** (180/pi)*

Where X is acceleration (*g*) in the surge axis, Y is acceleration (*g*) in the sway axis and Z is acceleration (*g*) in the heave axis.

ODBA and VeDBA are measures of dynamic body acceleration (DBA) in all three dimensions. DBA was calculated by smoothing data for each axis across a 1-second period to calculate the static acceleration, and then subtracting the static acceleration values from the raw acceleration values. ODBA is the sum of the dynamic body acceleration of the three axes, whereas VeDBA is the square root of the sum of the squares of dynamic body acceleration of the three axes (Qasem *et al.* 2012).

Assigning behaviours

We aimed to categorise kittiwake behaviours as: flying, on land, and on water, while human behaviours were categorised as: sitting, walking, and running. Assignment of behaviours was undertaken in a stepwise manner for both kittiwakes and humans. Metrics of the recorded acceleration data were selected based on how clearly they appeared to distinguish these target behaviours. Then, one behaviour at a time was separated from the others based on a threshold value calculated as an inter-peak frequency minimum of the metric employed. For the kittiwake data, flight behaviour was assigned first on the basis that this dynamic movement was likely to be more distinct than the stationary behaviours

of ‘on land’ or ‘on water’. The behaviours of ‘on land’ or ‘on water’ were then assigned to the remaining data. For human data, sitting was assigned before ‘walking’ and ‘running’ were assigned, again on the basis that this stationary behaviour was likely to be more distinct than the behaviours relating to two types of movement, walking and running.

Histograms plotted for the 10 metrics derived from the accelerometry data indicated that the standard deviation of the heave axis (SD_{Heave}) was bimodal for all kittiwakes (Supplementary material S2.1) and trimodal for all humans (Supplementary material S2.2). SD_{Heave} also had the greatest range of values when compared to other axes, indicating that movement across this axis was the most variable. For these reasons, as well as the use of heave in previous studies to identify flight behaviour (Wilson *et al.* 2006; Sato *et al.* 2008; Sakamoto *et al.* 2013; Vandenabeele *et al.* 2014), SD_{Heave} was the metric used to separate flight from non-flight behaviour in kittiwakes, and to separate sitting, walking and running in the human dataset. Furthermore, use of the standard deviation is likely to be more appropriate for identifying movement than just the raw acceleration values since raw acceleration during movement tends to oscillate and therefore likely overlap considerably with values recorded when the subject/participant is not moving (Figure 2). As histograms of SD_{Heave} for kittiwake data were bimodal, it was expected that non-flight behaviour would correspond to the lower values of SD_{Heave} and the higher values of SD_{Heave} would relate to flight. Therefore, the value of SD_{Heave} corresponding to the inter-peak frequency minimum between the first and second peak was determined and used as the threshold value to separate these behaviours. Histograms of the human data had trimodal distributions of SD_{Heave} and, considering the three behaviours recorded in the data correspond to different amounts of movement, it was assumed that each peak related to each of the behaviours. As such, the SD_{Heave} value corresponding to the inter-peak frequency minimum values between the first and second peak for each individual was determined and used as the

threshold value for separating sitting behaviour from walking and running. The value of SD_{Heave} corresponding to the inter-peak frequency minimum between the second and third peak was determined and used as the threshold value to separate walking and running.

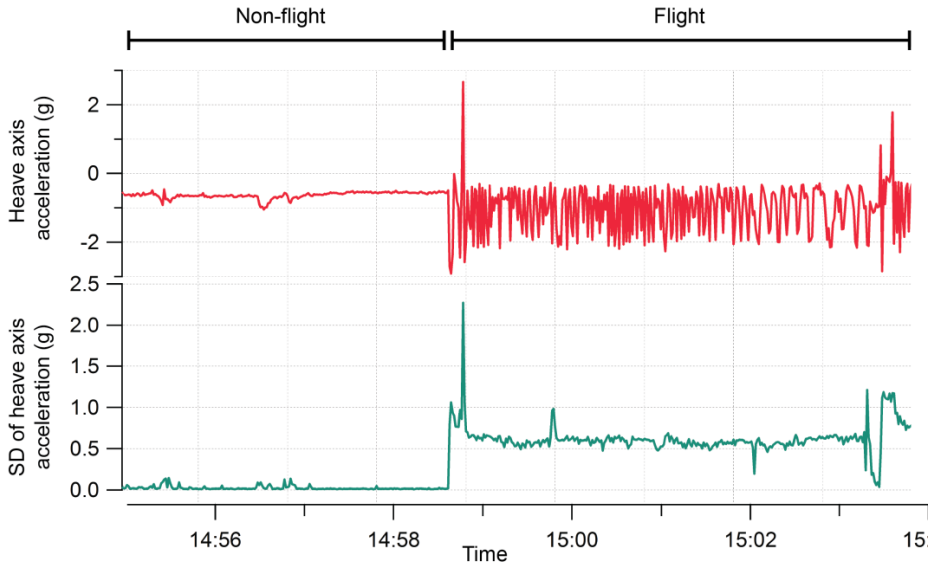

Figure 2.2. Raw acceleration values of the heave axis (upper trace) compared to the standard deviation of the heave axis (lower trace) from an accelerometer attached to a kittiwake.

For kittiwakes, the behaviours of 'on land' and 'on water' were assigned after flight had been assigned. Therefore, histograms of calculated metrics were reassessed with data corresponding to flight removed (Supplementary material S2.3). Body pitch was chosen as the most suitable metric to use to separate these remaining behaviours. This is because a kittiwake's body angle is likely to be different when on land compared to on water, due to the influence of nest angle as well as differences in body position arising from the range of movements; notably standing, incubating eggs and brooding chicks. Histograms of pitch showed clear peaks, indicating that individuals exhibited certain body pitch angles more predominantly than others during the data logger deployment (Supplementary material S2.3). The threshold value for separating 'on land' and 'on water' was determined as the

pitch value corresponding to the minimum frequency value between the first and second peak in the pitch histogram for each bird.

Cliff-nesting birds such as kittiwakes must fly to commute between land and water, thus to potentially further aid in the separation of the behaviours 'on land' and 'on water' this understanding of the underlying biology was incorporated in to the behavioural assignment process. To prohibit the possibility of an assignment of 'on water' directly following 'on land' and vice versa without a period of flight in between, the mean pitch was calculated between the end of each bout of flight and the start of the next (Figure 3). Data within the between flight bouts were then assigned as being 'on land' or 'on water' depending on the mean pitch value across the entire between flight period. These behaviours were assigned using the threshold determined by the inter-peak frequency minimum from the histograms of pitch before averaging.

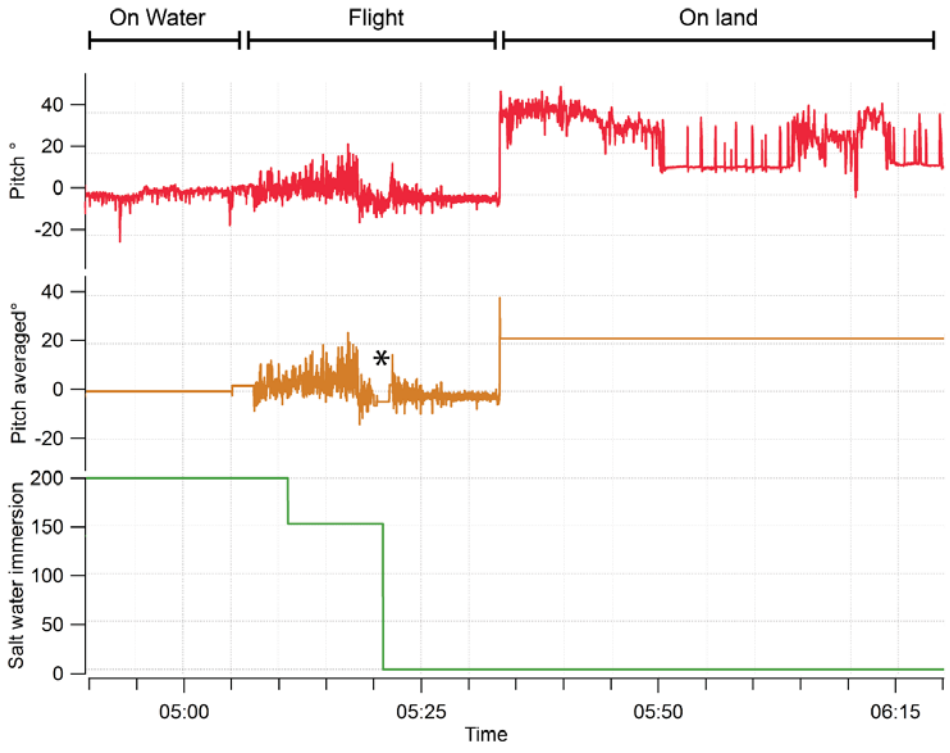

Figure 2.3. Pitch values of a kittiwake averaged to one second values (upper panel), and pitch values subsequent to the application of a correction factor averaging pitch between the end and start of flight periods (middle panel). Salt water immersion data, indicating on

water or out of water (lower panel). The asterisk indicates a brief period of resting on water in the middle of the flight section.

Validation

To determine the suitability of assigning behaviours by thresholds that correspond to inter-peak frequency minimum values of the chosen acceleration-derived metrics, the accuracy of behaviour assignments determined by a range of threshold values including the inter-peak frequency minimum values was calculated. To determine accuracy, the behavioural assignments across these threshold ranges were calculated during periods when the behaviours were known. This validation step is not integral to assigning behaviours and was used in this instance to test the effectiveness of the presented method.

For kittiwakes, 'flight' was assigned across a range of thresholds of SD_{Heave}, from 0-1 *g* at 0.02 *g* intervals. 'Flight' was assigned to data falling above each threshold. Accuracy of flight assignment dependent on the range of thresholds was calculated before assignment and subsequent validation of 'on land' and 'on water' behaviours. For assessing accuracy of assigning the behaviours 'on land' and 'on water' dependent on body pitch, the two behaviours were assigned across a range of pitch thresholds from -10° to 40° at 1° intervals. Data with pitch values below the threshold were assigned as 'on water', and data with pitch values above were assigned as 'on land'. The intervals chosen for the range of thresholds (0.02 g for SD_{Heave} and 1° for pitch) correspond to the bin sizes used for plotting the histogram. Bin sizes chosen resulted in smooth histograms with sufficient resolution to detect small changes in posture or amount of movement. An examination of the effect of bin size across orders of magnitude indicated that it made almost no difference to the accuracy of behavioural assignment (Supplementary material S2.4).

The known period of behaviour for kittiwake data used to calculate accuracy of assignment consisted of a two-hour period for each bird encompassing the three target behaviours (flight, on land, and on water) which was selected by eye and was manually assigned behaviours as done previously with similar datasets (McClune *et al.* 2014; Bidder *et al.* 2014). Due to the varied time-budgets of the individual birds, the amount of time within this two hour period spent doing each of the behaviours varied. Manual behavioural assignments were made using the programme IGOR Pro (Wavemetrics Inc., USA, 2000, version 6.3.5) with the Ethographer package (Sakamoto *et al.* 2009). Flight was assigned when traces of acceleration data displayed periodic fluctuations in dorso-ventral movement, as described previously in the literature (Wilson *et al.* 2006; Sato *et al.* 2008; Sakamoto *et al.* 2013; Vandenabeele *et al.* 2014), while assignment of 'on land' or 'on water' was informed by values from the salt water immersion logger. To calculate accuracy of assignment, we compared the assignment of behaviour for every second for each threshold value to these known behaviours during the validation period. We were then able to calculate the percentage of behavioural assignments which were correct for each threshold value in the series.

For the human data, SD_{Heave} was used to assign all three behaviours. For assessing the accuracy of assigning sitting behaviour, 'sitting' was assigned to data with an SD_{Heave} value below a threshold between 0-2 *g* at 0.02 *g* intervals. Once sitting was assigned using the inter-peak frequency minimum value of SD_{Heave}, the behaviours of walking and running were assigned to the remaining data across a range of standard deviation thresholds. The thresholds ranged from the standard deviation value identified for separating sitting behaviour (~0.1 *g*) up to a standard deviation value of 2.0 *g,* at 0.02 *g* intervals. As with the kittiwake data, intervals tested corresponded to the bin size of the histograms (0.02 *g*), with the chosen bin sizes resulting in smooth histograms. Furthermore, bin size again made

very little difference to the accuracy of behavioural assignment (Supplementary material S2.4). Walking was assigned to data with a standard deviation below each threshold, while running was assigned to data above the threshold. Accuracy of human data assignments was easier to measure as during data collection exact activities were recorded by participants thus behavioural assignments were fully validated. Accuracy was calculated as the percentage of behavioural assignments from this method which were the same as the known, recorded behaviours. As deployments were relatively short the full dataset was compared to each threshold dependent assignment, giving a measure of accuracy across the full deployment.

All data analysis was conducted in R statistical software (R Development Core Team, 2008), other than visualisation of accelerometry and immersion data for validation, which was conducted using the Ethographer package in Igor Pro (Wave Metrics). Script required to execute this method in R is provided along with a link to an example data set for a kittiwake (Supplementary material S2.5).

Results

Kittiwakes

A clear bimodal distribution was present in histograms of SD_{Heave} for all birds (Figure 4). Separating flight behaviour from non-flight behaviour in kittiwakes using SD_{Heave} was highly accurate. By separating flight behaviour using the inter-peak frequency minimum threshold, the mean (±1sd) accuracy of assignment of flight versus non-flight behaviour across all birds was 97.9 ± 1.7% (Figure 5). Although this value did not correspond to the mean highest possible accuracy calculated across the full range of SD_{Heave} thresholds (98.3 ± 1.3%), the difference in accuracy was small (mean difference: 0.4 ± 0.3%; maximum difference: 0.9%).

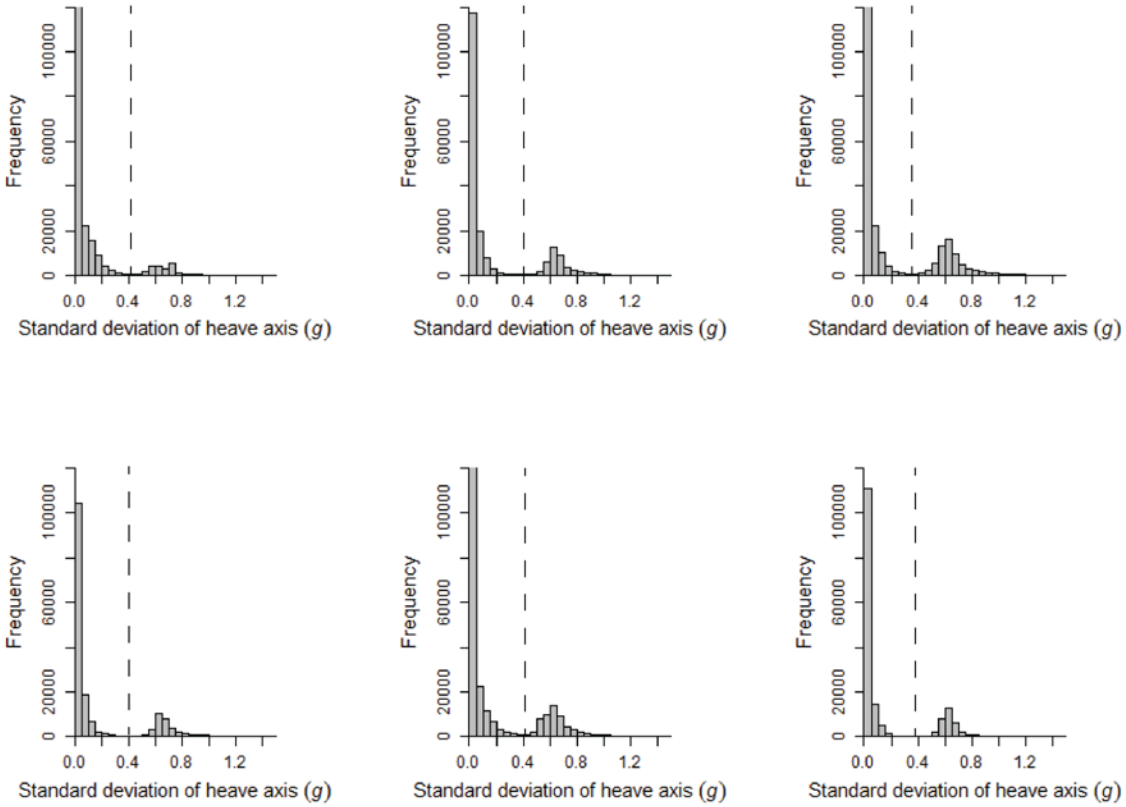

Figure 2.4. Histograms of the standard deviation of the heave axis data recorded during accelerometer deployments on each of six kittiwakes. The dashed line indicates the inter-peak frequency minimum.

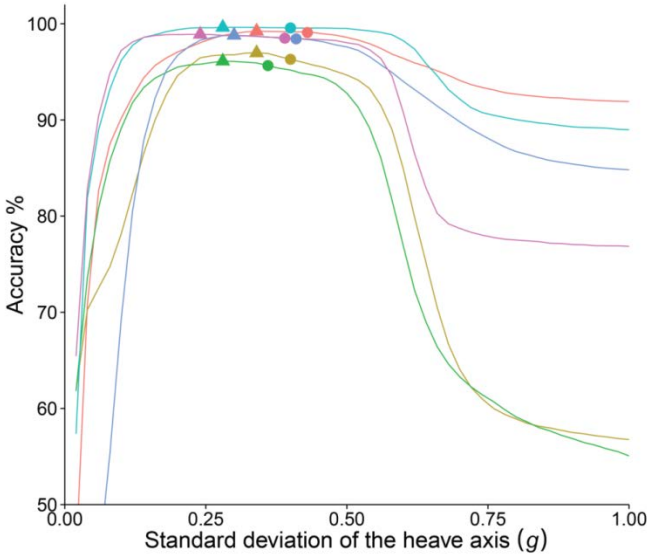

Figure 2.5. Percentage accuracy of flight assignment plotted against the standard deviation of the heave axis used as a threshold value used to assign the behaviour. Each line represents an individual kittiwake. Circles indicate accuracy at the threshold value corresponding to the inter-peak frequency minimum from the histogram of standard deviation of the heave axis (see Figure 4), triangles indicate the value corresponding to the threshold value that achieves maximum accuracy.

Histograms for body pitch of the bird did not display such a clear or consistent distribution as histograms for SD_{Heave} (Figure 6). Three of the birds had a distribution with two peaks in frequency, whereas the other three had three peaks. The degree to which these peaks were distinct, and at which point they occurred in the data varied between the individuals. However, averaging pitch values between flight periods further separated the peaks (Figure 7) and, despite the variability between individuals, separating the behaviours of 'on land' and 'on water' by pitch was consistently highly accurate. By separating these behaviours using the threshold corresponding to the inter-peak frequency minimum value between the first and second peak of each pitch histogram, accuracy of assignment was 90.4 ± 8.9% when behaviours were assigned based on initial pitch values, and 97.5 ± 2.1% when

assigning behaviours based on the pitch values averaged between bouts of flight. The maximum possible accuracy of assignment by separating these behaviours by pitch was 95.9 ± 3.6% when assigned by initial pitch values and 97.7 ± 2.0% when pitch was averaged (Figures 8a & 8b). In addition, the range of pitch values at which accuracy of assignment remained above 95% increased by an average of 8.5° ± 6.0° after assigning behaviours based on average pitch between bouts of flight. This is shown by the elongated plateaus of higher accuracy values in figure 8b compared to figure 8a.

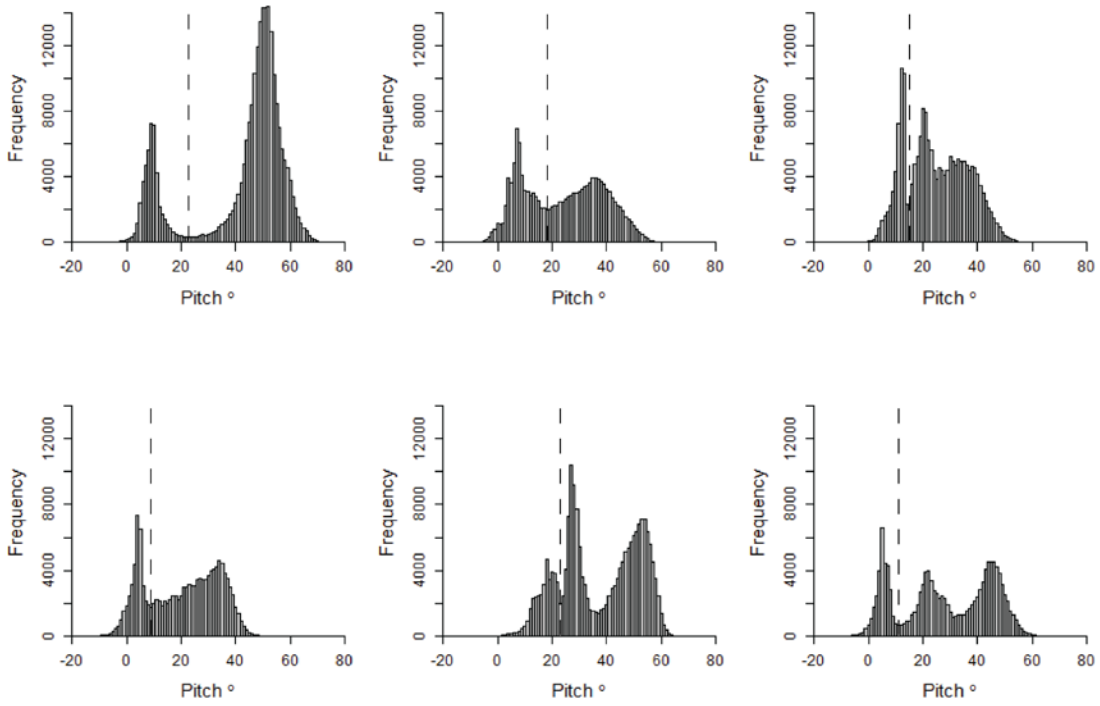

Figure 2.6. Histograms of the pitch angle of six kittiwakes while instrumented with an acceleration data logger. Data already assigned as flight are excluded. The dashed line indicates the inter-peak frequency minimum between the first and second peak.

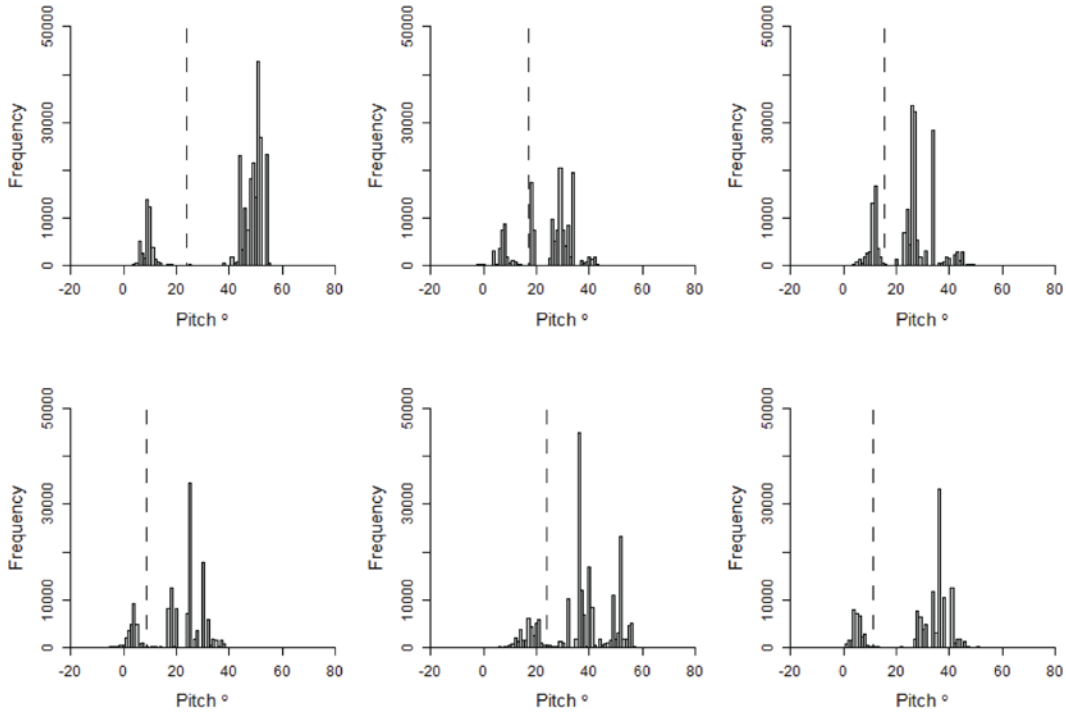

Figure 2.7. Histograms of pitch for each kittiwake after averaging pitch values between flight periods. The dashed line indicates the inter-peak frequency minimum between the first and second peak present in the histogram before averaging (Figure 6).

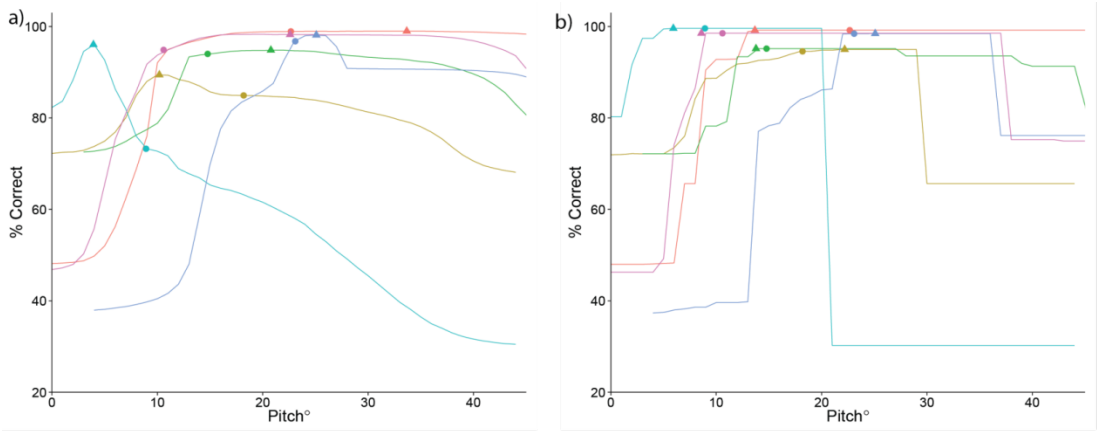

Figure 2.8. (a) Percentage accuracy of behaviour assignments after determining whether the bird was on land or on water against body pitch. (b) Percentage accuracy of behaviour assignments against body pitch after pitch values were averaged between bouts of flight. Circles indicate accuracy at the threshold value corresponding to the inter-peak frequency minimum between the first and second peak from the histogram of pitch for each bird, while triangles indicate the value corresponding to the threshold value that achieves maximum accuracy.

Humans

A trimodal distribution was present in histograms of SD_{Heave} for all human participants (Figure 9). In this instance, SD_{Heave} was used to differentiate between all three behaviours exhibited (sitting, walking and running). Separating sitting behaviour from any movement using the inter-peak frequency minimum of the first and second peak, assignment accuracy was 98.75 ± 0.68% (Figure 10a). The highest possible percentage accuracy was higher than this at 99.11 ± 0.46%; the mean difference in accuracy was therefore small, at 0.36 ± 0.30%. Running and walking behaviours were separated after sitting data were already assigned. By using the inter-peak frequency minimum value between the second and third peak of the standard deviation histogram to determine the threshold value, average assignment

accuracy was 98.26 ± 0.88% (Figure 10b). The highest possible accuracy regardless of frequency of standard deviation values was 98.42 ± 0.86%.

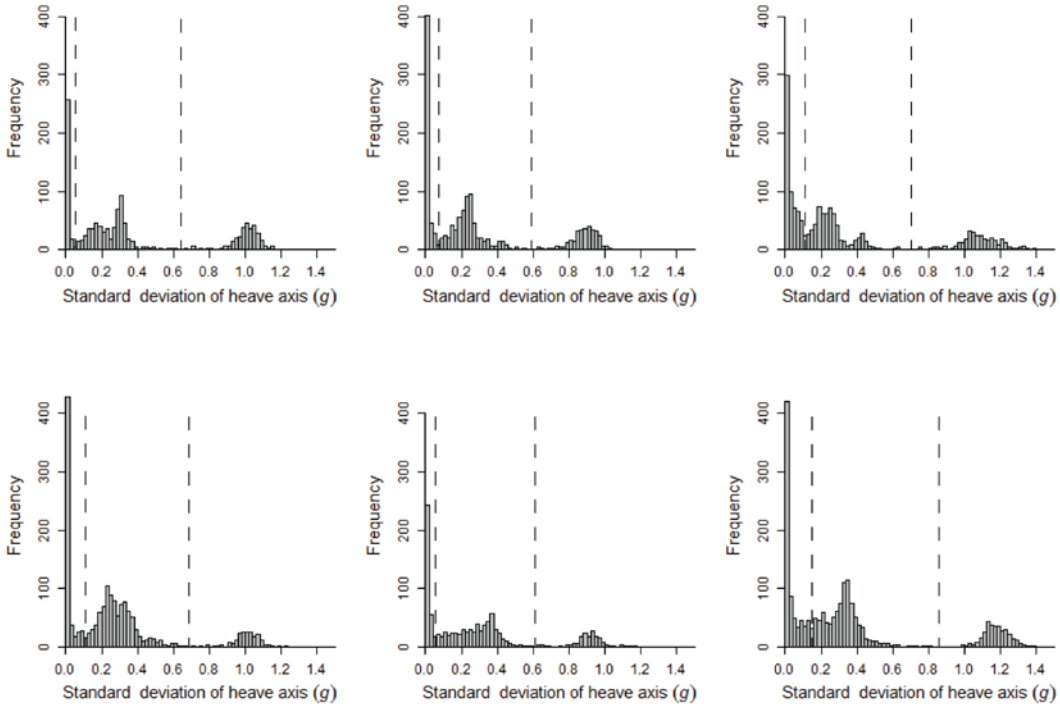

Figure 2.9. Histograms of the standard deviation of the heave axis data recorded during acceleration data logger deployments on six human participants. Dashed lines indicate the inter-peak frequency minimum between peaks.

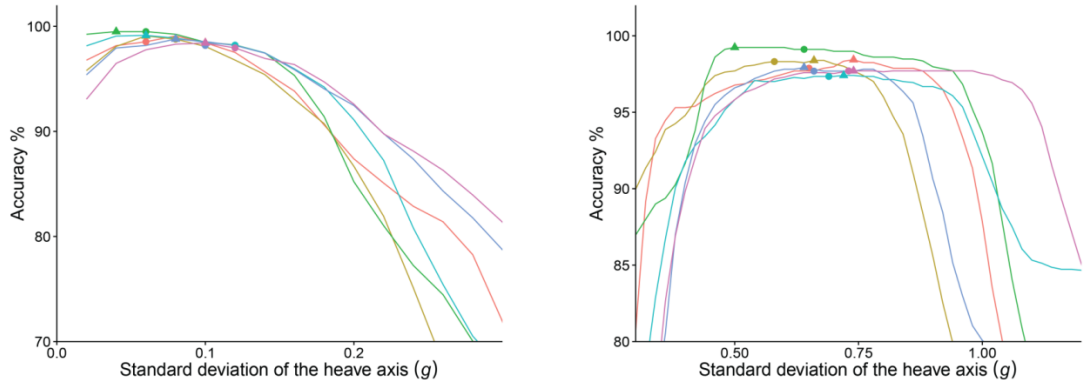

Figure 2.10. Percentage accuracy for all human participants against the standard deviation of the heave axis for a) identifying sitting and b) for separating walking and running behaviours. Circles indicate accuracy at the threshold value corresponding to the inter-peak frequency minimum between a) the first and second, and b) the second and third peak from the histogram of standard deviation of the heave axis for each participant. Triangles indicate the value corresponding to the threshold value that achieves maximum accuracy

Discussion

The analysis presented shows that by assigning behaviours using objectively determined thresholds from histograms of readily calculated metrics of accelerometry data, it is possible to classify coarse-scale behaviours in both kittiwakes and humans to a high degree of accuracy. Estimated percentage accuracy of assignments of approximately 97% for kittiwake data and 98% for human data is very high, and such accuracy is comparable to methodologies achieving the highest rates of coarse-scale behaviour assignment (Nathan *et al.* 2012; McClune *et al.* 2014; Bidder *et al.* 2014). It should however be noted that a direct comparison to other methods has not been made.

The purpose of this study was to test and provide a method for assigning behaviours which can be readily applied to other datasets. Existing studies have used similar threshold based

approaches to classify behaviour (Yoda *et al.* 2001; Gómez Laich *et al.* 2009; Nathan *et al.* 2012; Kawabata *et al.* 2014). However, the threshold values provided in these cases have tended to be study-specific, with little information given as to how such values were determined. In the present study, it has been demonstrated that separation of coarse-scale behaviours can be achieved by assigning behaviours based on an objectively identified threshold value between peaks within histograms of suitable metrics of acceleration. By defining these thresholds as the value corresponding to the minimum frequency of data points falling between peaks (the inter-peak frequency minimum), accuracy was almost as high as the maximum possible accuracy calculated for separating behaviours. As determining the inter-peak frequency minimum is an objective stage of the method, the small difference in accuracy achieved when compared to the maximum possible accuracy achievable through an iterative approach of testing a range of threshold values justifies the application of this approach. This is especially true for studies where validation is not possible. Using objectively determined thresholds for separating behaviours is also advantageous in that they are specific to each individual while being simple to calculate. This reduces potential assignment error of using one threshold for all individuals which may arise from individual variation in the metrics used to separate behaviours. Furthermore, demonstration of the consistency of this approach for two distinct model species with contrasting behavioural modes implies that the method is likely suitable for a range of other species. In addition, unlike with more complex approaches incorporating machine learning for classifying behaviour, which represent and classify data as points in space based on summary statistics (Bidder *et al.* 2014), the method outlined here relies on assigning behaviours based on metrics relating to the position of the subject (body pitch) or its amount of movement (standard deviation of an axis). This aspect of the method does incorporate some subjectivity into the method, at the point of choosing how many behaviours to classify and which metrics to use, but results in the process of assignment

being readily understandable and justifiable in relation to the target species' biology. With such metrics relating to behaviour in many taxa, and the method being simple to execute, application of this approach on other species should be straightforward. Indeed, by providing the script to apply this method, we hope it will be further tested on acceleration data from species with different modes of behaviour to those presented here.

In some cases it may be that the shapes of histograms of chosen metrics do not correspond clearly with the number of behaviours being assigned. This was evident when using body pitch to separate the behaviours of 'on land' and 'on water' for kittiwakes, which was initially the least accurate stage of behavioural assignment. This was due to the pitch of the bird sometimes overlapping when on land and on water. Such overlap of pitch is likely to be due to the potentially small difference in orientation of the birds when on the nest in relation to their position on water. Pitch measurements were also likely to vary due to individual variation in amount of movement when on land (i.e. when the bird was mainly on the nest). However, the simplicity of the metrics used to separate these behaviours allowed for the inclusion of a biological argument to further enhance accuracy of assignments, namely that to transition between being on land and on water requires a period of flight between the two. Averaging pitch between bouts of flight further separated out the range of pitch values associated with the bird being on land and the range of values associated with the bird being on water, thus increasing accuracy.

Although pitch has been used to differentiate behaviour in seabirds before (Shepard *et al.* 2008; Gómez Laich *et al.* 2009), species used in such studies have tended to have a much more defined difference in body angle between behaviours; for example penguins and shags, which tend to be in either prone or upright positions during particular behaviours (Yoda & Ropert-Coudert 2007; Gómez Laich *et al.* 2009). By averaging pitch between flight

periods this method can potentially be applied to other species which either overlap in pitch between behaviours or have less pronounced differences between body orientations across different behaviours. In addition to, and perhaps more important than, the increase in accuracy resulting from averaging pitch between flight bouts, the range of pitch values at which accuracy remained high increased in all birds. This effectively reduces the importance of identifying an exact threshold value for separating behaviours as long as the value identified falls in the range corresponding to high accuracy of assignment. While it is unlikely that such an argument can be applied to all taxa, where possible the inclusion of such biologically grounded arguments should be considered before resorting to more complex approaches of behavioural classification.

An unexpected consequence of our approach is that variation in frequency histograms of metrics such as body pitch could also be used as a diagnostic tool for identifying even coarser scale behavioural or life-history states such as the stage of the breeding cycle of a target individual. The kittiwake individuals in this study which displayed three peaks in the pitch histograms were all rearing chicks while those with two peaks were incubating eggs. This is consistent with incubating birds spending a larger proportion of their time sitting (incubating) whereas chick rearing birds switch between sitting (brooding) and standing. This potential application of acceleration metric histograms could be especially viable given the continuing miniaturisation and increased longevity of data logging devices (Hunt & Wilson 2012), which should enable longer term deployments on free-ranging animals.

Validation of behaviour assignments

Validation of behavioural assignments on wild animals is often unobtainable. However, the approach of simultaneous deployment of two different types of logger, as demonstrated with coupling accelerometers with salt water immersion loggers on kittiwakes in this study,

offered a source of sample validation. Such coupling of devices increases the confidence of interpreting information from datasets which may otherwise be difficult to justify (Wilson *et al.* 2008; Dean *et al.* 2013; Watanabe & Takahashi 2013). Furthermore, by allowing estimation of accuracy across a range of threshold values, this approach has enabled confirmation that frequency distributions (represented by histograms) of metrics of accelerometry data can indeed correspond to distinct behaviours. Although validation of behavioural assignments would be desirable for each study employing the accelerometry technique, it is not always possible. Using data from similar species, or even captive animals, to inform behavioural assignments (Campbell *et al.* 2013) has been suggested in the absence of validation, however the approach we present here offers a solution which is not reliant on a source of validation, or sourcing other datasets. The lack of dependence upon validation therefore broadens the applicability of this approach.

Conclusion

There are numerous methods available for classification of behaviour from accelerometry data (e.g. Shepard *et al.* 2008; Nathan *et al.* 2012). The present approach offers a method informed by sound biological reasoning for classifying coarse-scale behaviours by means of objectively determined threshold values, which is easy to understand, visualise and undertake. We hope that where appropriate, future studies can employ the method described here, thus bringing a degree of consistency to studies in which behaviours are assigned to acceleration data. We especially hope for this method to be applied to and tested on a wider range of species exhibiting different types of behaviours. Where a more detailed analysis is required, the approach presented here offers a platform prior to further interrogation of the data. Further analysis could, for example, involve isolating flight behaviour to calculate wingbeat frequency or other such metrics calculable from high-resolution accelerometry data (Spivey & Bishop 2013).

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Supplementary materials S2

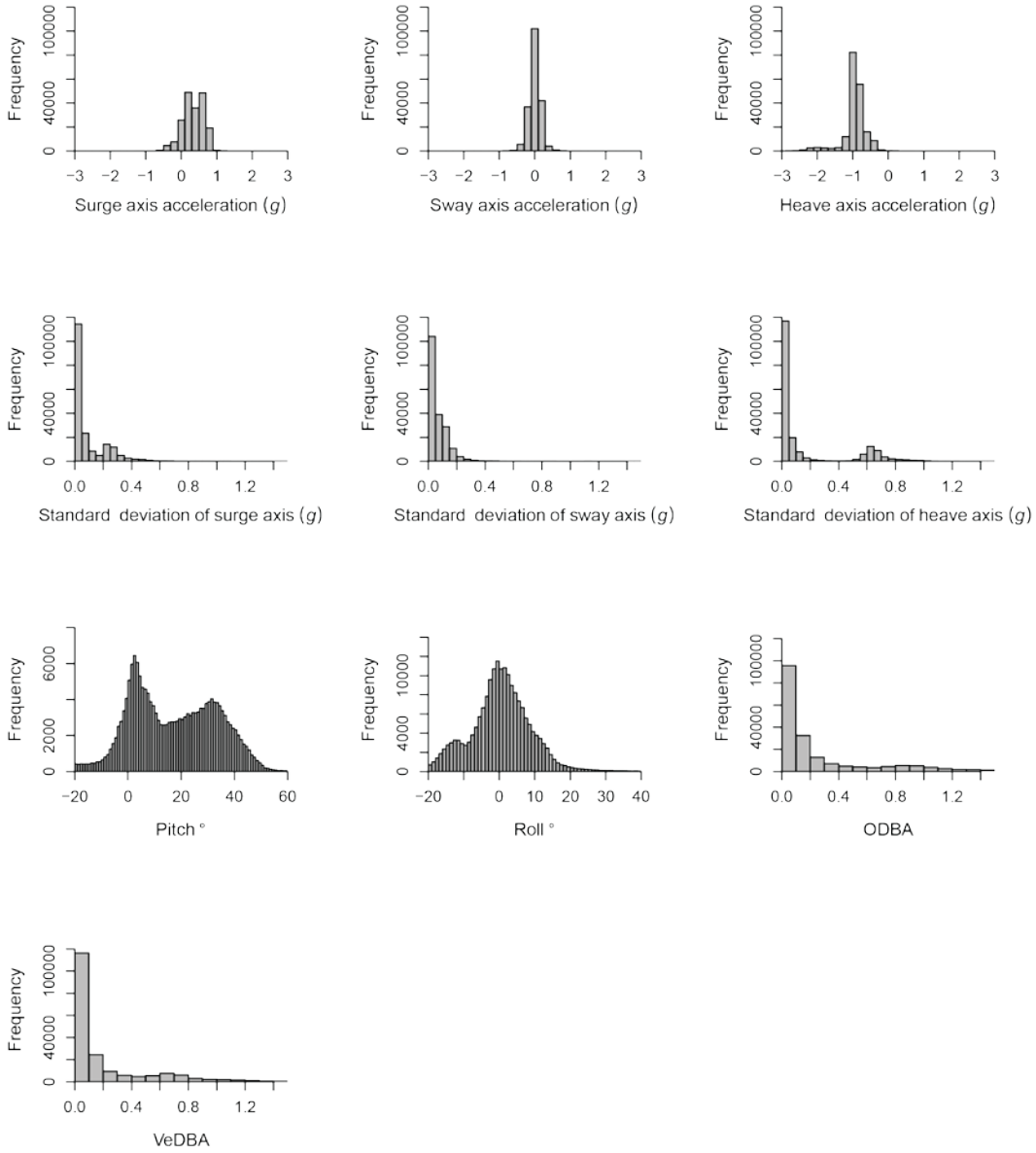

Figure S2.1. Histograms for calculated metrics of accelerometry from one kittiwake.

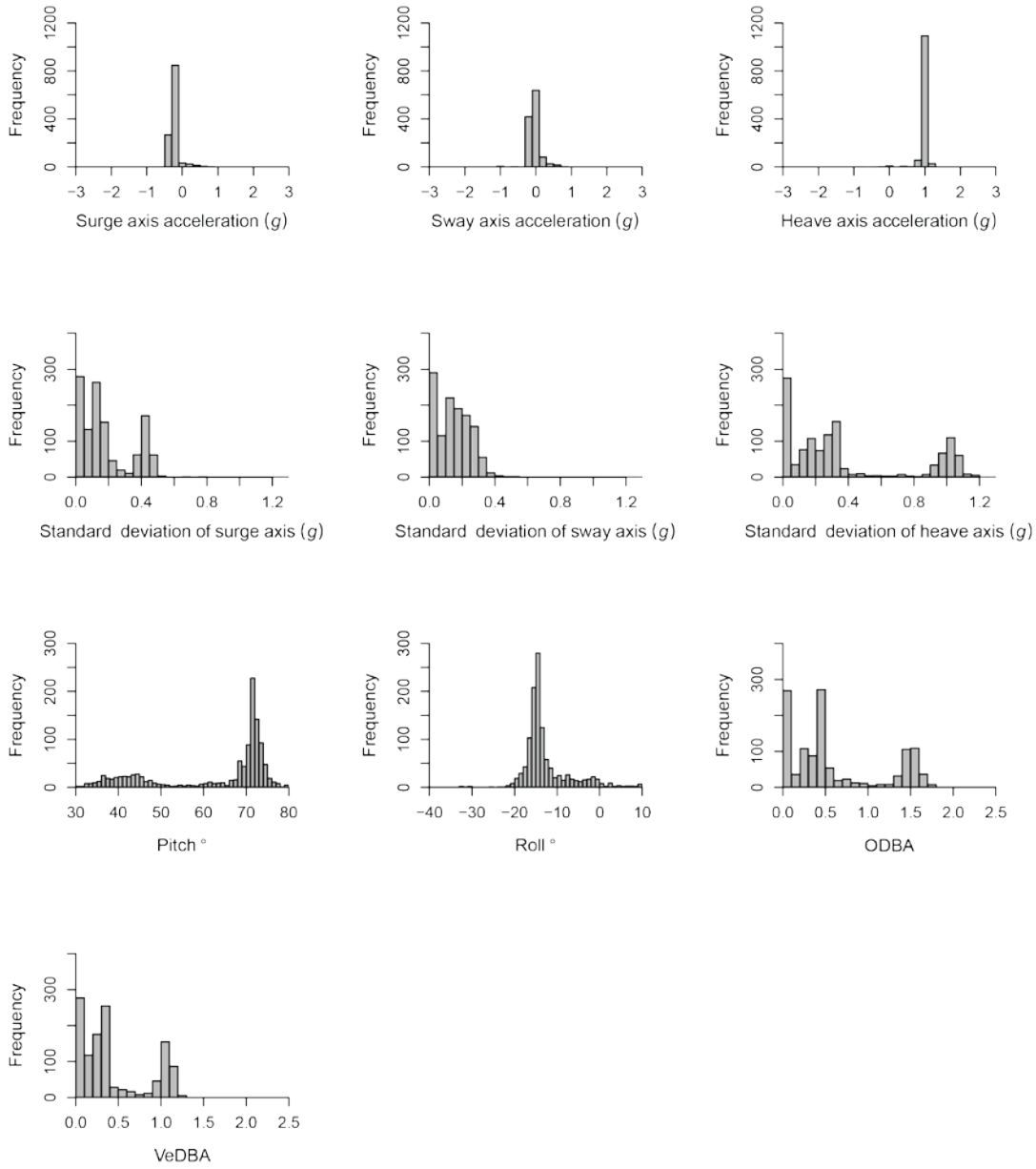

Figure S2.2. Histograms for calculated metrics of accelerometry from one human participant.

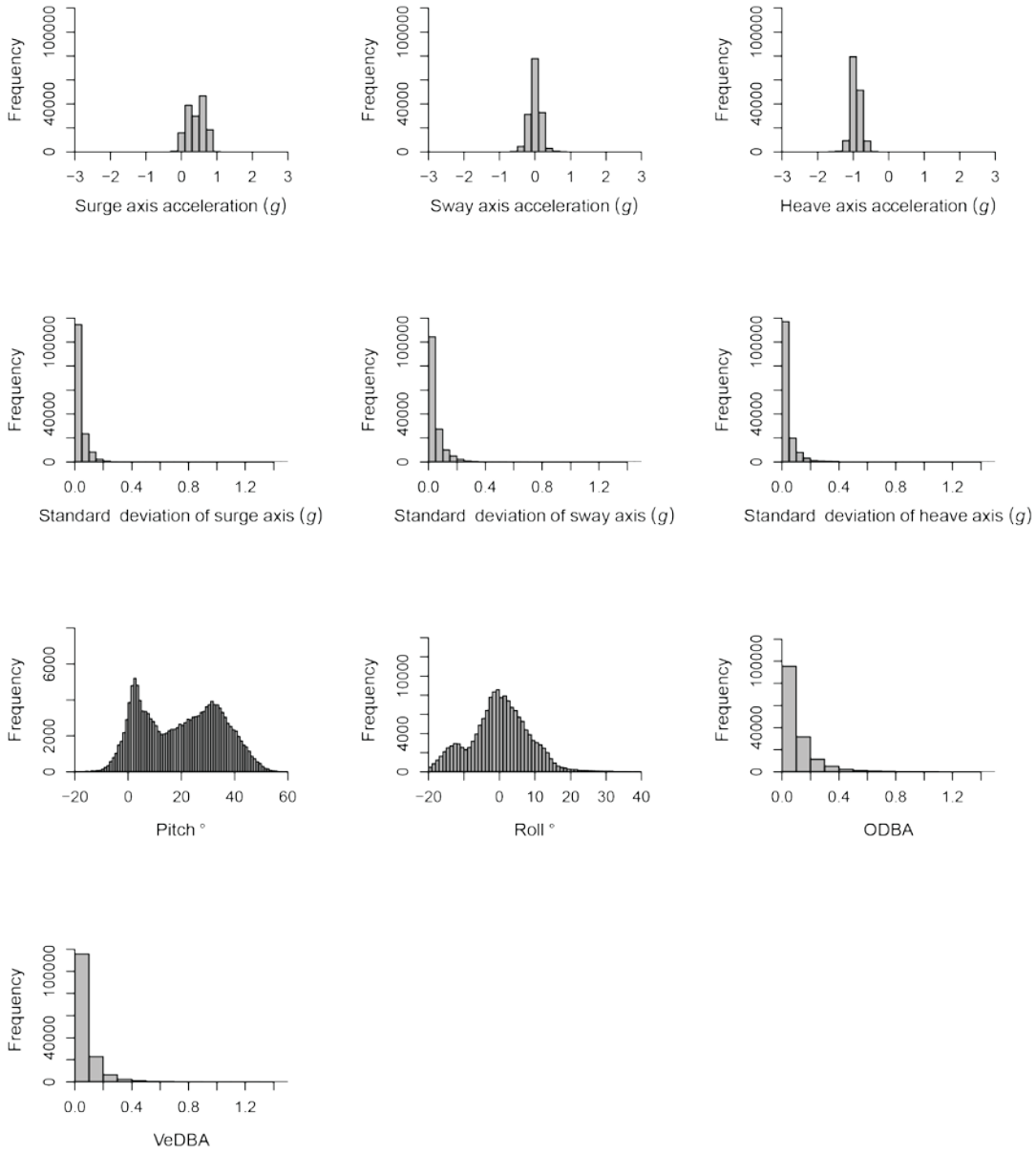

Figure S2.3. Histograms for calculated metrics of accelerometry from one kittiwake after data assigned as flight were removed.

Table S2.4. Accuracy of assignments for both species and all three behaviours depending on bin size used in the histograms generated to inform behavioural assignments.

	Standard deviation of heave axis bin size						**Pitch bin size**				
	0.01	**0.02**	**0.05**	**0.1**	**0.2**	**0.5**	**0.5**	**1**	**2**	**5**	**10**
	% correct assignment						% correct assignment				
Bird ID											
EG79073	98.9	98.9	98.7	98.8	98.3	98.1	98.8	98.8	98.9	98.9	98.9
EL48867	95.4	95.7	95.0	96.0	95.3	96.4	93.8	93.8	93.7	93.8	94.3
EL48898	96.0	96.1	96.0	95.8	95.2	96.2	95.5	95.5	95.8	95.8	94.5
ET41812	99.5	99.5	99.5	99.4	99.5	99.5	99.5	99.5	99.5	99.5	99.5
EX41203	96.0	96.0	96.1	96.2	96.1	97.0	95.8	95.8	96.5	96.6	74.6
EX41446	98.4	98.4	98.4	98.5	98.4	98.7	98.4	98.4	98.4	98.4	75.2
Human ID											
1	94.9	94.9	97.9	95.1	75.8	81.1					
2	98.4	98.4	98.2	92.7	96.9	70.0					
3	97.5	94.1	98.0	95.2	97.6	74.7					
4	97.6	97.8	98.2	95.6	76.9	84.1					
5	99.4	99.6	99.6	99.6	99.3	97.0					
6	96.0	97.7	97.3	96.2	60.4	86.2					

S2.5 The script developed to apply the behaviour assignation method.

```
##### This script calculates metrics of accelerometry, plots histograms of these metrics
###### and makes behavioural assignments based on these histograms. Copy and paste
####this code into the R console to implement it or alternatively download from
##http://onlinelibrary.wiley.com/doi/10.1002/ece3.1660/abstract
# An example dataset can be found at:
#http://onlinelibrary.wiley.com/store/10.1002/ece3.1660/asset/supinfo/ece31660-sup-
0004-#AppendixS6.csv?v=1&s=2ed1a0ef08ee0f0b3a5d4a8d4dc136bd1a97a61d

# to reset R removing assigned function
rm(list=ls())
library("zoo",)
options(digits.secs=2)
getwd()

#Input data should consist of one csv file of time, X,Y,Z, where X is assumed to be
acceleration
# in the surge channel, Y is acceleration in sway, and Z is acceleration in heave.

Data<-read.csv(file.choose(),stringsAsFactors=FALSE)
head(Data)
tail(Data)
str(Data)

freq<-25 #The Frequency of accelerometry data
```

```
secs<-1 # the number of seconds over which to calculate the desired metrics.The
manuscript says to use 1 second intervals,
#but to capture gliding flight as well I've found that a longer period is needed.
numrows<-freq*secs # the number of rows required to calculate metrics over the chosen
period.
##Calculate rolling means over a set period.
Data$meanX=rollapply(Data$X,numrows,mean,fill=NA)#25 = number of cells to average
across, change to desired time considering sampling frequency.
Data$meancent=rollapply(Data$X,numrows,mean,fill=NA)#25 = number of cells to average
across, change to desired time considering sampling frequency.
Data$meanY=rollapply(Data$Y,numrows,mean,fill=NA)#25 = number of cells to average
across, change to desired time considering sampling frequency.
Data$meanZ=rollapply(Data$Z,numrows,mean,fill=NA)#25 = number of cells to average
across, change to desired time considering sampling frequency.
#Calculate rollingstandard deviation over a set period.
Data$SDX=rollapply(Data$X,numrows,sd,fill=NA)#25 = number of cells to average across,
change to desired time considering sampling frequency.
Data$SDY=rollapply(Data$Y,numrows,sd,fill=NA)#25 = number of cells to average across,
change to desired time considering sampling frequency.
Data$SDZ=rollapply(Data$Z,numrows,sd,fill=NA)#25 = number of cells to average across,
change to desired time considering sampling frequency.
##Calculate pitch
Data$pitch<-atan((Data$X/(sqrt((Data$Y*Data$Y)+(Data$Z*Data$Z)))))*(180/pi);
#Calculate roll
Data$roll<-atan((Data$Y/(sqrt((Data$X*Data$X)+(Data$Z*Data$Z)))))*(180/pi);
#####Calculate ODBA and VeDBA####
```

```
Data$RunningAx=rollapply(Data$X,numrows,mean,fill=NA)

Data$RunningAy=rollapply(Data$Y,numrows,mean,fill=NA)

Data$RunningAz=rollapply(Data$Z,numrows,mean,fill=NA)

####Calculates DBA for each axis.

Data$StaticX<-Data$X-Data$RunningAx

Data$StaticY<-Data$Y-Data$RunningAy

Data$StaticZ<-Data$Z-Data$RunningAz

Data$ODBA<-abs(Data$StaticX)+abs(Data$StaticY)+abs(Data$StaticZ)

Data$Vedba<-sqrt((Data$StaticX^2)+(Data$StaticY^2)+(Data$StaticZ^2))



Data<-subset(Data,

select=c(NewTime,X,Y,Z,meanX,meanY,meanZ,SDX,SDY,SDZ,pitch,roll,ODBA,Vedba))

head(Data)

####Subset to 1-second intervals

Data$NewTime2<-as.POSIXct(Data$NewTime,format ="%Y-%m-%d %H:%M:%S")

library("plyr")

Data2<-ddply(Data, .(NewTime2), function(x) x[13,])

Data2<-Data2[-1,] # removes first row which is likely to be NA, depending on interval of

metric calculation.This will need to be run a few times until there are no NAs, depending on

the time used to average/ calculate SD over.

head(Data2)

Data2<-Data2[-nrow(Data2),]

tail(Data2)

#####Plot histograms of the calculated metrics.
```

```
##Change bin sizes and range as shown with the SDZ metric to fully explore the data.
maxSDZ<-max(Data2$SDZ)+0.1 # have to add a small amount for the breaks to work.
minSDZ<-min(Data2$SDZ)-0.1
interval<-0.02 # change depending on bin size required.
hist(Data2$SDZ,breaks=seq(minSDZ,maxSDZ, by=interval),)
str(Data2$SDZ)
print(sum(is.na(Data2$pitch)))
print(sum(is.na(Data2$SDZ)))
Data2$pitch<- na.locf(Data2$pitch,fromLast=FALSE)
Data2$SDZ<- na.locf(Data2$SDZ,fromLast=FALSE)
head(Data2)
hist(Data2$meanX)
hist(Data2$meanY)
hist(Data2$meanZ)
hist(Data2$SDX)
hist(Data2$SDY)
hist(Data2$SDZ)
hist(Data2$pitch)
hist(Data2$roll)
hist(Data2$ODBA)
hist(Data2$Vedba)

###### Identify peaks in the data and calculate the inter-peak frequency minimum by
taking the metric value
###corresponding to the minimum frequency count between peaks.
SDZhist<-hist(Data2$SDZ,breaks=seq(minSDZ,maxSDZ, by=interval),)
```

```
SDZhist
mids<-SDZhist$mids
counts<-SDZhist$counts
SDZhistdata<-data.frame(mids,counts) # make a dataframe from the histogram data
SDZhistdata
#Identify the Inter-peak frequency minimum value(s) In this example the IPFM is calculated
between a value above 0.1 and below 0.5
#change this depending on where the peaks fall in your dataset.
#If this returns numerous values, take the average.
firstpeak<-0.1 # set a value corresponding to the  value with the highest frequency at the
first peak. This does not have to be accurate.
secondpeak<-0.6 # set a value corresponding to the  value with the highest frequency at
the second peak. This does not have to be accurate.
SDZhistdata<-subset(SDZhistdata,mids>firstpeak&mids<secondpeak)
IPFM<-SDZhistdata[which(SDZhistdata$counts==min(SDZhistdata$counts)),1]
IPFM


##Assign behaviours based on the IPFM. Use numbers to indicate discrete behaviours. In
this example, 1 indicates flight,
##2 indicates being on water, and 3 indicates being on land.


for(i in 1:length(Data2))
{
  Data2$behaviour[Data2$SDZ>IPFM]<-1
}
#Assign a number to data not falling within the identified threshold.
```

```
Data2[is.na(Data2)] <- 4


#The next round of behavioural assignment can then take place. e.g.after plotting
histograms with
#data belonging to the first behavioural assignment having been removed and the IPFM for
the second
#metric having been identified
# The example below incorporates the above round of assignment as well as another set of
arguments which depends on
#the IPFM found from the metric 'pitch'
head(Data2)
######For pitch
minpitch<-min(Data2$pitch)-1
minpitch
maxpitch<-max(Data2$pitch)+1
maxpitch
interval<-1
hist(Data2$pitch[Data$SDZ>IPFM],breaks=seq(minpitch,maxpitch, by=interval))
pitchhist<-hist(Data2$pitch,breaks=seq(minpitch,maxpitch, by=interval))
pitchhist


mids<-pitchhist$mids
counts<-pitchhist$counts


pitchhistdata<-data.frame(mids,counts) # make a dataframe from the histogram data
pitchhistdata
```

```
#If this returns numerous values, take the average.
firstpeak<-10 # set a value corresponding to the  value with the highest frequency at the
first peak. This does not have to be accurate.
secondpeak<-50 # set a value corresponding to the  value with the highest frequency at the
second peak. This does not have to be accurate.
pitchhistdata<-subset(pitchhistdata,mids>firstpeak&mids<secondpeak)

IPFMpitch<-pitchhistdata[which(pitchhistdata$counts==min(pitchhistdata$counts)),1]
IPFMpitch

for(i in 1:length(Data2))
{
  Data2$behaviour[Data2$SDZ>IPFM]<-1 # 1 =flight
  Data2$behaviour[Data2$SDZ<IPFM & Data2$pitch<=IPFMpitch]<-2 # 2 = on water
  Data2$behaviour[Data2$SDZ<IPFM & Data2$pitch>IPFMpitch]<-3 # 3 = on land
}
#Assign a number to data not falling within the identified threshold.
Data2[is.na(Data2)] <- 4

####The following is the script used for averaging pitch between flight periods in the
manuscript.
head(Data2)
Data2[1,16]<-1

rval<-as.numeric(row.names(Data2))
Data2$b0row<-rval
```

```
for(i in 1:length(Data2)){

  Data2$b0row[Data2$behaviour==2]<-NA

  Data2$b0row[Data2$behaviour==3]<-NA

}

Data2$b0na<- na.locf(Data2$b0row,fromLast=FALSE)

for(i in 1:length(Data2)){

  Data2$b0na[Data2$behaviour==1]<-NA

  Data2$b0na[Data2$behaviour==4]<-NA

}

library(plyr)

avg<-ddply(Data2, .(b0na), transform, pitchavg=mean(pitch))

avg<-avg[order(avg$NewTime),]

Data2$pitchavg<-avg$pitchavg

tail(Data2)

Data2 <- subset(Data2, select = -c(NewTime2,b0row,b0na))
```

```
#####Behaviours can then be reassigned using the same process as above, but with
assignments now dependent on the average pitch values.
for(i in 1:length(Data2))
{
  Data2$behaviour[Data2$SDZ>IPFM]<-1
  Data2$behaviour[Data2$SDZ<IPFM & Data2$pitchavg<=IPFMpitch]<-2
  Data2$behaviour[Data2$SDZ<IPFM & Data2$pitchavg>IPFMpitch]<-3
}

head(Data2)

Data<-subset(Data2, select=c(NewTime, behaviour,pitch,SDZ))
head(Data)
tail(Data)
write.csv(Data,"Accelerometerwithbehaviours.csv",row.names=FALSE)
```

Chapter 3

Energetic consequences of time-activity budgets for a breeding seabird

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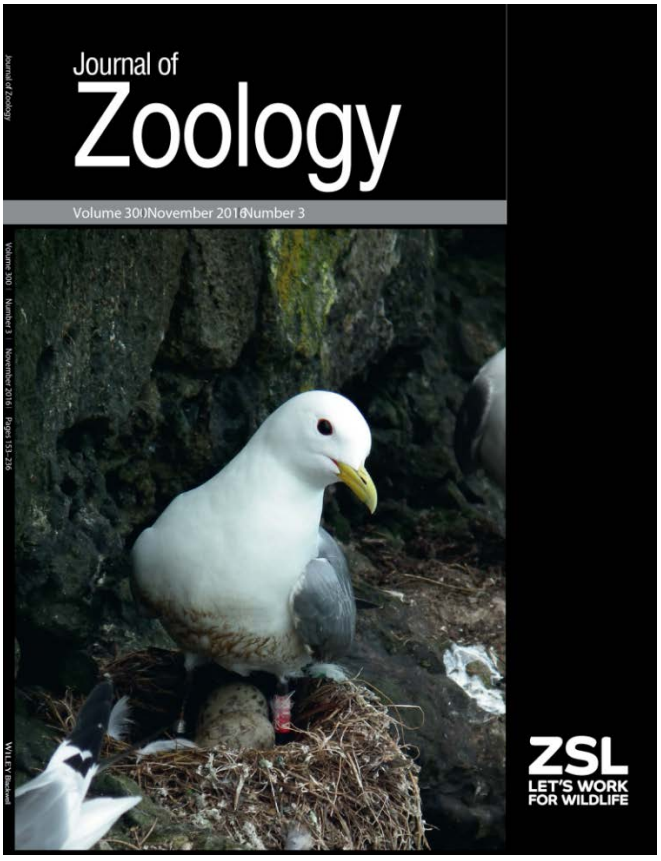

Author contributions: PMC, LGH, JAG & PJAS designed the study, PMC, JAG & SD conducted fieldwork, JPYA provided biologgers, PC analysed data and wrote the manuscript with support from LGH, JAG, PJS & JPYA.

Abstract

How animals allocate their time to different behaviours has important consequences for their overall energy budget and reflects how they function in their environment. This potentially affects their ability to successfully reproduce, thereby impacting their fitness. We used accelerometers to record time-activity budgets of 21 incubating and chick-rearing kittiwakes on Puffin Island, UK. These budgets were examined on a per day and per foraging trip basis. We applied activity-specific estimates of energy expenditure to the kittiwakes' time-activity budgets in order to identify the costs of variation in their allocation of time to different behaviours. Estimates of daily energy expenditure for incubating kittiwakes averaged 494±20 kJ d^{-1} while chick-rearing birds averaged 559±11 kJ d^{-1}. Time-activity budgets highlighted that kittiwakes did not spend a large proportion of their time flying during longer foraging trips, or during any given 24-hour period. With time spent flying highlighted as the driving factor behind elevated energy budgets, this suggests behavioural compensation resulting in a possible energetic ceiling to their activities. We also identified that kittiwakes were highly variable in the proportion of time they spent either flying or on the water during foraging trips. Such variation meant that using forage trip duration alone to predict energy expenditure gave a mean error of 19% when compared to estimates incorporating the proportion of a foraging trip spent flying. We have therefore highlighted that trip duration alone is not an accurate indicator of energy expenditure.

Introduction

During their breeding periods, many animals must increase their foraging effort in an attempt to provide enough food not only for their own survival but also for the survival and growth of their offspring (Grémillet 1997). As movement accounts for a large proportion of energy expenditure in many free-ranging animals (Brit-Friesen *et al.* 1989), this elevated foraging effort impacts the energy budgets of individuals. Thus how animals allocate their time to different behaviours during the breeding period can be a key component to their eventual reproductive success and fitness (Gittleman & Thompson 1988).

Understanding the interactions between behaviour, energetics, and fitness is a key consideration for comprehending the roles of organisms in their ecosystems (Tomlinson *et al.* 2014). However, free-ranging animals are often difficult to observe over long periods of time without interruption. Seabirds exemplify this difficulty, with individuals often foraging far out at sea, where directly observing their behaviour is highly impractical. Conventionally, presence or absence of individuals at their nest has been used to indicate how they allocate their time during the breeding season (Granadeiro *et al.* 1998; Lewis *et al.* 2001), yet this approach lacks detailed information regarding activity when away from the nest. As time away from the nest comprises of a variable combination of time spent in either active behaviours (such as flight or foraging) or resting, allocation of time to activity within this period is likely to be of major energetic importance. Using animal-borne data loggers such as accelerometers, which measure an animal's body acceleration continuously, it is now possible to collect continuous measurements of the behaviour of individuals to generate detailed time-activity budgets regardless of location (e.g. Shepard *et al.*, 2008; Halsey *et al.*, 2009b).

While the biological implications of variation in time-activity budgets are informative alone, it is even more informative to estimate how differences in time allocation to behaviour relate to energy expenditure. Currently the most prominent approaches for estimating energy expenditure *in-situ* are the doubly-labelled water (DLW) method and the heart rate method. Although these techniques have greatly enhanced our understanding of energy expenditure in wild animals, they do have limitations, notably the DLW method has poor temporal resolution (Butler *et al.* 2004; Shaffer 2011) and the heart rate method generally requires surgical implantation of a data logger (Butler *et al.* 2004). Alternatively, by combining time-activity budgets with either laboratory or model derived estimates of activity-specific energy expenditure, time-energy budgets can be constructed (Goldstein 1988). Such an approach is not novel in principle, yet the inclusion of accelerometry derived time-activity budgets now allows for this approach to be applied to continuous, high-resolution behavioural information from highly mobile animals (Shamoun-Baranes *et al.* 2012). This alternative approach then allows estimation of energy expenditure of free-ranging animals at a finer temporal scale than the DLW method, and in a less invasive manner than the heart-rate method.

In this study, we combine accelerometer-derived time-activity budgets with published values of activity-specific metabolic costs to estimate the energy expenditure of free-ranging black-legged kittiwakes (*Rissa tridactyla*). Kittiwakes are a suitable species on which to apply this approach as they have a relatively simple repertoire of coarse-scale behaviours, consisting of flight, being on water, and attending the nest; these behaviours are readily identifiable from accelerometry traces (Collins *et al.* 2015). To date, energy expenditure of kittiwakes has been estimated numerous times with the DLW method (Gabrielsen *et al.* 1987; Thomson *et al.* 1998; Golet *et al.* 2000; Jodice *et al.* 2002, 2003, Welcker *et al.* 2009, 2014; Schultner *et al.* 2010), highlighting variation within and between

individuals and populations, as well as showing that time away from the colony is an important component of total daily energy expenditure (DEE) (Fyhn *et al.* 2001). Furthermore, in a study by Welcker et al. (2010) which employed the DLW method, kittiwakes exhibited remarkably similar DEE across years with different prey availability. They therefore posited that kittiwakes were operating at an intrinsic energy ceiling, whereby individuals apparently had a limit to the amount of energy they expend (Drent & Daan 1980). It is likely that kittiwakes exhibit behavioural compensation, whereby they adjust time spent in more energetically demanding activities to limit energy expenditure (Elliott *et al.* 2014a), however, the poor temporal resolution of the DLW method coupled with a lack of continuous behavioural data has largely inhibited the possibility of identifying evidence for this. In this study, by deploying accelerometers on both incubating and chick-rearing kittiwakes, we quantify how kittiwakes allocate their time, and what the energetic consequences of variation in time allocation are. By linking behaviour to energy expenditure we set out to identify if there is evidence for behavioural compensation.

Methods

Data collection

Tri-axial accelerometers (X8m-3 Gulf Coast Data Concepts, LLC; recording range ±8 *g*, resolution: 0.001 *g*, weight: 14 g), set to record at 25 Hz, were deployed on 50 kittiwakes over three breeding seasons. Accelerometers were attached to feathers on the centre of the backs of individuals using clothed black Tesa® tape. The placement of the accelerometer was kept as consistent as possible across all birds. Mean body mass was 365±31 g (mean±SD), ranging from 310 – 435 g, with data loggers weighing on average 3.8±0.3% of body mass. 28 accelerometers were retrieved, of which 21 were functioning correctly. Of these 21 accelerometers, 17 were from individuals during the early chick-rearing stage (chicks less than 10 days old), and 4 were from adults at the late incubation

stage. Accelerometers were deployed on birds at a similar point within the incubation or chick-rearing process as energy expenditure changes dependent on time into these stages (Fyhn *et al.* 2001). Accelerometers that were not retrieved were either deployed on individuals which evaded recapture, or had fallen off before retrieval was attempted. Accelerometers not removed would have fallen off within two weeks. Deployment time for recaptured birds averaged 58±22 h and ranged from 23 – 114 h, during which time birds exhibited apparently normal breeding behaviour, including nest attendance (comprising of care of eggs or chicks) or absence from the nest (most likely on foraging trips). Fieldwork was carried out on Puffin Island, North Wales in July 2012, July 2013 and July 2014. All work was carried out under Countryside Council for Wales permit numbers (37727:OTH:SB:2012, 44043:OTH:SB:2013, 53628:OTH:SB:2014).

Behavioural assignments

To generate time-activity budgets, acceleration data were assigned to three coarse-scale behaviours: "nest attendance", "on water", and "flying". Although finer-scale behaviours such as foraging, preening, and courtship are exhibited by kittiwakes, the amount of time these behaviours take up is relatively little (Jodice *et al.* 2003). As per Collins et al. (2015), behaviours were assigned using a simple method that categorises different activity types based on readily calculable metrics indicating body orientation or amount of movement. This method has been shown to give high accuracy (>95%) of coarse-scale behaviour assignments in kittiwakes (Collins *et al.* 2015). Behaviours of "nest attendance" and "on water" were assigned depending on the body angle of the bird; periods when the bird was at a lower angle were assigned as "on water", and periods at which the bird was at a higher body angle were identified as being on land. The body angle thresholds at which these behaviours were separated were specific to each individual. When classified as on land, based on observations of their behaviours, the birds were assumed to be attending their

nest, and were thus assigned the behaviour "nest attendance". Flight was assigned based on the standard deviation of acceleration values in the heave axis, with higher values indicating movement in this channel relating to flight. Flight was not separated into flapping or gliding, although inspection of acceleration traces suggested that the kittiwakes flapped much more than glide.

Time-activity budgets

We constructed time-activity budgets at two scales of interest; daily and complete foraging trips. For each day and each foraging trip we determined the amount and proportion of time spent on the three coarse-scale behaviours. For daily time-activity budgets, only records consisting of 24 hours of continuous data starting at midnight were used. The sample size for incubating birds was 3 days' worth of data from 3 individuals, and that for chick-rearing birds was 25 days' worth of data from 17 individuals. Foraging trips were defined as a period in which the bird flew from the land, spent time on water, and then returned to the land, with trips varying in duration. Only trips over 30 minutes were used, to exclude periods when birds might have left the land for reasons other than foraging (such as researcher disturbance, or predator avoidance (Collins *et al.* 2014)). In total 146 trips were identified and analysed. Trips were further separated into two types; those which started one day and finished the next were assigned as overnight trips (n=18), while those starting and finishing on the same day were assigned as day trips (n=128).

Time-energy budgets

To estimate the energy expenditure for the behaviours "nest attendance" and "on water" we used the intraspecific allometric equations for resting metabolic rates of these behaviours reported in Humphreys et al. (2007). For estimating the energy cost of flight we used the modelling software Flight 1.25 (http://www.bristol.ac.uk/biology/people/colin-j-

pennycuick/index.html, Pennycuick (2008)). We used the default values for a kittiwake wingspan (0.947 m) and aspect ratio (9.44 m^2) and input mass per bird from our data. We included a payload of 14g to account for the accelerometer and set altitude at 10m above sea level. Standard errors of energy cost estimates were calculated through 10 000 iterations of bootstrapping with replacement from the distribution of the activity-specific energy costs (n=21).

To estimate the most accurate total DEE possible for each bird we input individual kittiwake mass into our equations for activity-specific energy expenditure and combined these activity-specific costs with each individual's time-activity budget. These values are used to report estimates of DEE for the population for the incubation and chick-rearing periods overall. To get an estimate of DEE which indicates how time spent in each behaviour alone influences energy expenditure, we estimated activity-specific energy costs based on the mean kittiwake mass of 365g and combined these with each individual's time-activity budget. This method was also used to estimate foraging trip energy expenditure. For estimates using mean mass, energy expenditure while attending the nest was calculated to be 13.6±1.2 kJ h^{-1}, energy expenditure while on water was 18.8±3.0 kJ h^{-1}, and energy expenditure for flying was 48.24±5 kJ h^{-1}. Estimating energy expenditure for these behaviours based on mean mass is justified as preliminary analysis showed no relationship between body mass and time-activity budgets.

Statistical analysis

A Welch's t-test (used due to unequal variances) was applied to test for differences in DEE between the three study years. As DEE did not significantly differ between years ($t_{13.191}$ =-0.494, p=0.6297) we pooled all data for analysis. A Welch's t-test was also used to test for differences in DEE between incubating and chick-rearing birds. To analyse differences in

foraging trip durations and proportion of trips spent in flight between breeding stages and trip type, generalised linear mixed models (GLMMs) including these variables and the interaction between them were constructed. A GLMM was also constructed to analyse the effect of forage trip duration on the proportion of trip spent in flight. Due to each kittiwake undertaking numerous foraging trips, in all GLMMs individual bird identity was assigned as a random factor. Models with foraging trip duration as the response variable were constructed using a Gaussian family with a log link due to the response variable conforming to assumptions of normality, while models with proportion of trip spent in flight as the response variable used a binomial family with logit link, as this response variable did not conform to assumptions of normality. To assess the accuracy of using foraging trip duration alone to predict energy expenditure, the difference between estimated energy expenditure for each foraging trip to that predicted by a general linear model between forage trip duration and energy expenditure was calculated.

P-values below 0.05 were deemed to be significant, although our analysis places a greater emphasis on graphical representation of the data due to the imprecise nature of P-values (Halsey *et al.* 2015) and low sample sizes in some aspects of the study. All means are presented ±1 standard error unless otherwise stated. All data analysis was conducted in R statistical software version R 3.2.1 (R Development Core Team, 2015) using 'glmmPQL' from the 'MASS' package.

Results

Time-activity budgets

Over a 24-hour period, incubating and chick-rearing kittiwakes differed in how they allocated their time to the three behaviours (Figure 3.1.). Incubating kittiwakes spent a similar percentage of their time attending their nest as they spent on water (41.7±18.4 and 43.8±20.3%, respectively), and proportionally less of their time in flight (14.5±3.3%). Chick-

rearing kittiwakes spent more of their time attending their nest (58.9±2.4%), with time spent on water taking up the least amount of their daily time budget (13.5±5.8%). Chick-rearing kittiwakes spent almost twice as much of their day in flight than incubating kittiwakes did (27.6±2.1%).

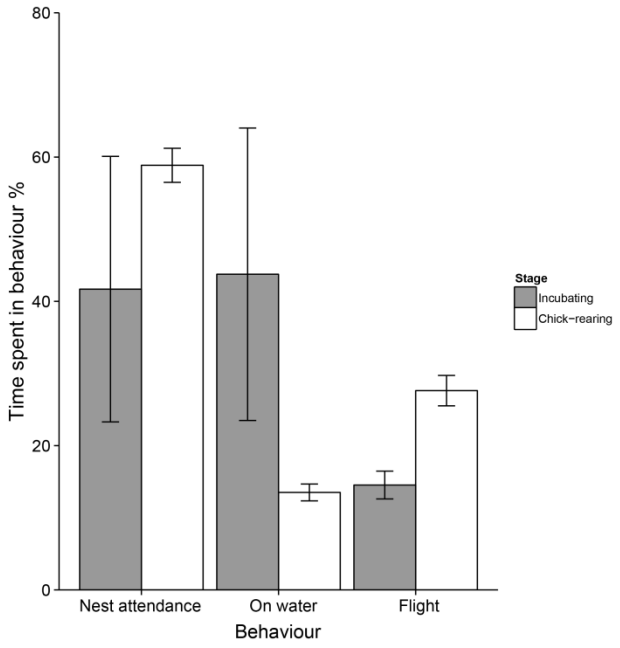

Figure 3.1. Mean ± SE daily percentage of time spent undertaking three recorded coarse-scale behaviours for incubating (n=3) and chick-rearing kittiwakes (n=25). Only days with 24 hours-worth of data were used.

Time spent on foraging trips, and the proportion of time spent either flying or on water within these trips, varied considerably both within and between birds. Duration of foraging trips was highly variable for all kittiwakes (Figure 3.2a); mean duration of foraging trips for incubating kittiwakes was 3.10±0.73 h, ranging from 0.53–9.22 h (n= 17), while the mean foraging trip duration for chick-rearing kittiwakes was 2.70±0.20 h, ranging from 0.50-10.83 h (n=129). These differences were not significant, however (t_{19} = 1.14, p=0.267). Trip duration was significantly longer for overnight trips compared to trips starting and ending

on the same day (Figure 3.2b) (t_{19} = 13.48, p<0.001), with daytrips averaging 2.07±0.15 h (range 0.50– 7.88 h, n=128) and overnight trips averaging 7.60±0.47 h (range 3.67–10.83 h, n=18). There was no significant interaction between breeding stage and trip type in relation to trip duration (t_{123} = -0.60 p=0.552).

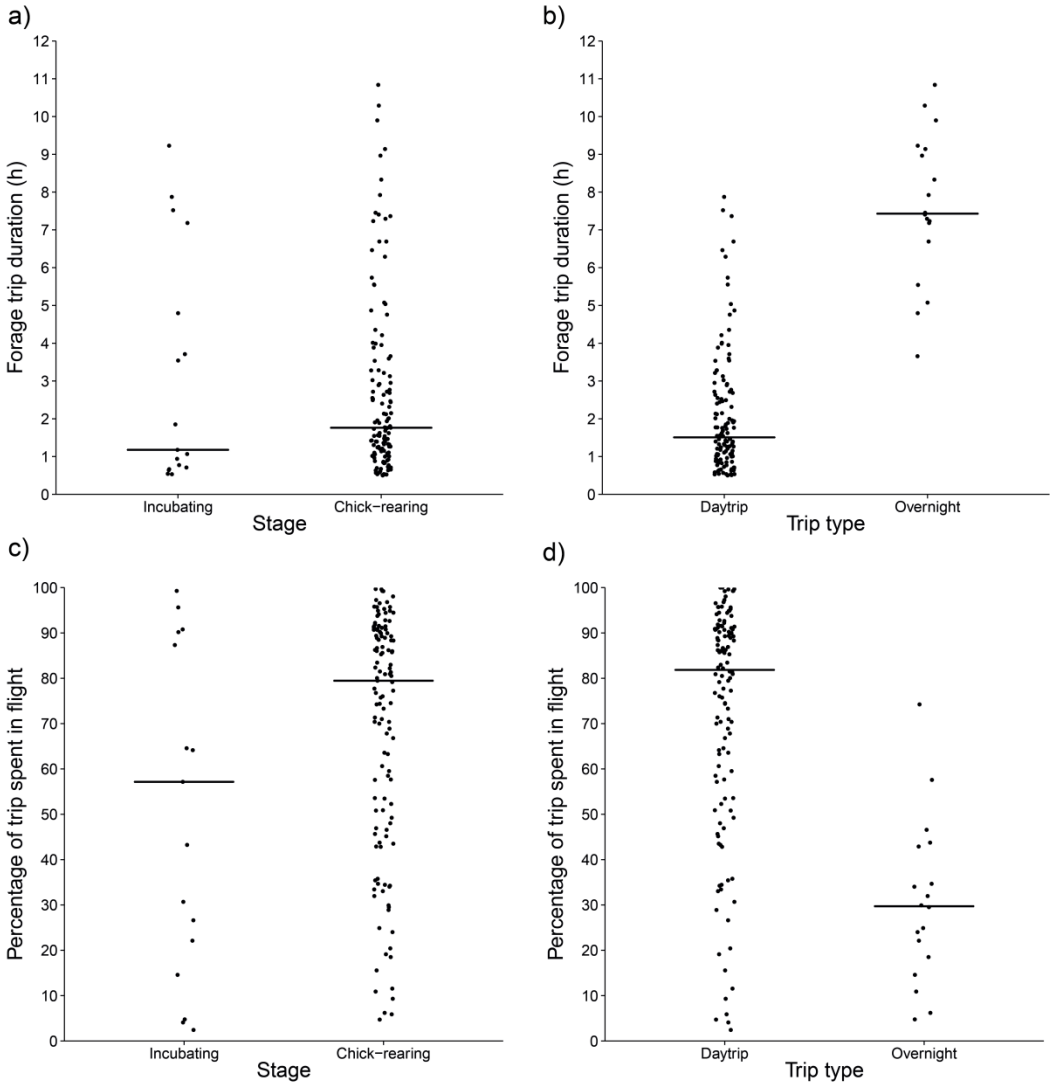

Figure 3.2. Duration of foraging trip dependent on breeding stage (a) and trip type (b), and proportion of individual foraging trips spent flying dependent on breeding stage (c) and trip type (d). Black dots indicate individual foraging trips, black lines indicate the median value.

The proportion of time spent flying during each trip also varied considerably between trips (Figures. 3.2c & 3.2d). For incubating kittiwakes the mean proportion of foraging trips spent flying was 53±9% (ranging from 24-99%, n=17) while for chick-rearing kittiwakes the mean was 69±2% (ranging from 47-99%, n=129). As with foraging trip duration, percentage of foraging trip spent flying did not differ significantly between breeding stages (t_{19} = -1.55, p=0.137). Trip type (day trip or overnight trip) had a significant effect on the proportion of time spent flying over the foraging trip, with the proportion of time spent flying during daytrips (mean= 72±2%, ranging from 2-99%, n=128) being significantly greater (t_{123} = -6.78 p<0.001), than proportion of time spent flying during overnight trips (mean = 31±4%, ranging from 30-74%, n=18). There was no significant interaction between breeding stage and trip type in relation to proportion of time spent flying (t_{123} = -0.35 p=0.725).

Energy expenditure

Estimated individual DEE averaged 552±12 kJ d^{-1} (n=28). The average for incubating kittiwakes was 494±20 kJ d^{-1} (n=3), which was 13% lower than chick-rearing kittiwakes which averaged 559±11 kJ d^{-1} (n=25) however these estimates did not differ significantly (t_5=2.0, p=0.10). Individual DEE values (range 358±31 - 745±67 kJ d^{-1}) as well as mass and time spent in each behaviour are presented in Appendix 3.1.

Using estimates of energy expenditure based on average mass, due to the higher energy cost per unit time of flight, kittiwakes that spent a greater proportion of the day flying had higher DEE (Figure 3.3.). As a result, high variation in the proportion of time individuals spent flying across the day drove the variability in estimated DEE (Figure 3.3.).

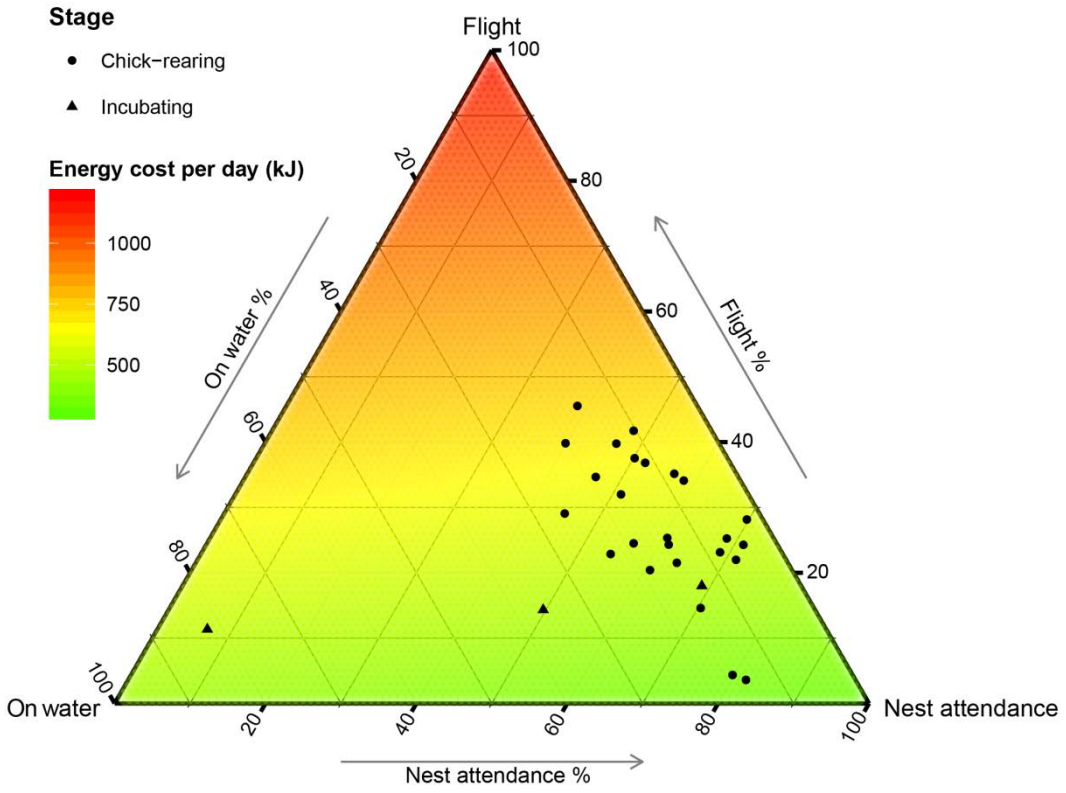

Figure 3.3. The daily energy expenditures of kittiwakes of average mass, dependent on allocation of time to nest attendance, being on the water, and flying. Each black symbol represents a full 24-hour period of recorded activity from an individual incubating (triangle) or chick-rearing (circle) kittiwake. Percentage of time spent in each activity should be read parallel to the direction of the tick marks for each axis, respectively.

As foraging trips were highly variable in both duration and allocation of time to either flying or resting on water, the estimated energy expenditure across those trips also varied widely, from 14±1 kJ to 368±19 kJ, averaging 103.1±7 kJ (n=153) (Figure 3.4.). Expressed as rate of energy expenditure, on foraging trips kittiwakes expended between 19.5±1.4 and 48.2±2.2 kJ h^{-1}, averaging 38.2±1.9 kJ h^{-1}. Of all 153 foraging trips measured, 62% of them cost less than 100 kJ of energy, with 84% costing less than 200 kJ. Shorter foraging trips were highly variable in time spent flying, but had the highest recorded percentage of time spent flying

across foraging trips (Figure 3.4.). Overall, proportion of time spent in flight decreased significantly with duration (t_{124} = -5.52, p<0.001). As foraging trips which lasted longer tended to have a lower proportion of time spent in flight, the hourly rate of energy expenditure for such trips was lower than for shorter trips. No kittiwakes exhibited extremely high percentages of time spent in flight during foraging trips of longer duration, with the maximum estimated energy expenditure of 368±19 kJ corresponding to a trip lasting 10.29 h, of which 57.6% (5.92 h) was spent flying.

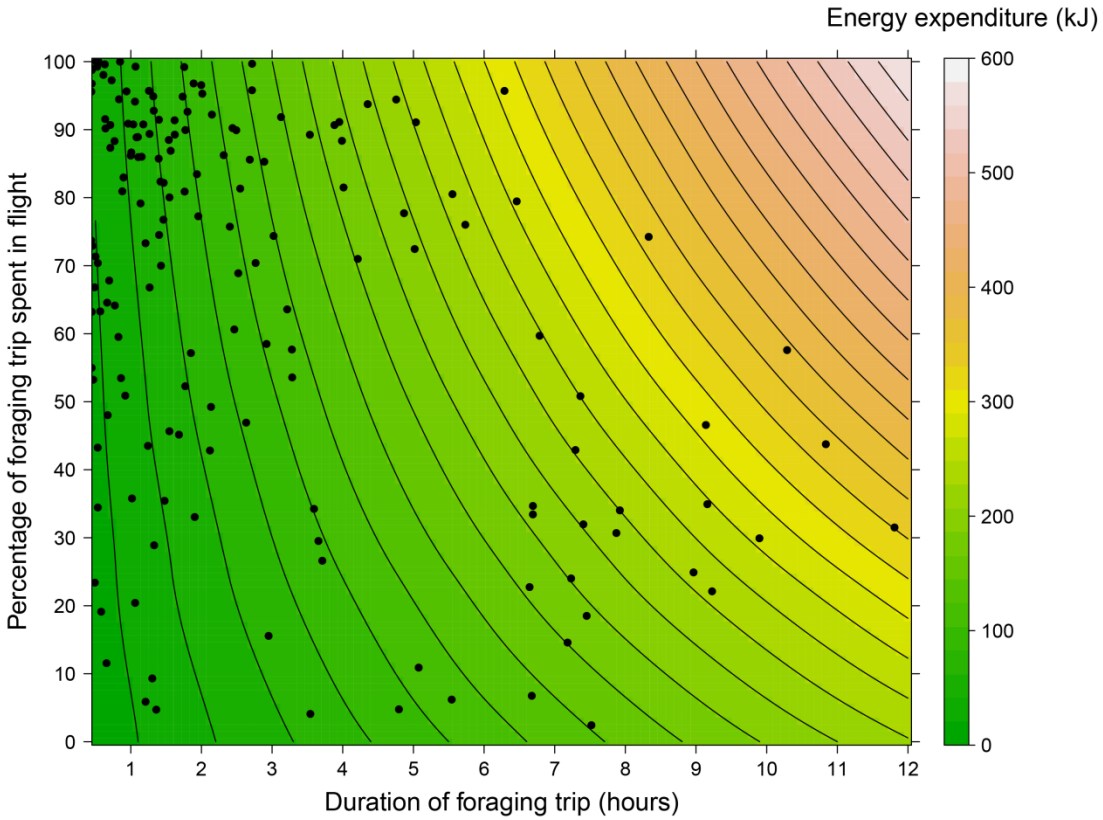

Figure 3.4. Total energy cost (kJ) of foraging trips dependent on percentage of trip spent flying in relation to duration of foraging trip. Black dots indicate values from individual foraging trips from 21 kittiwakes.

Foraging trip duration alone was a poor predictor of estimated foraging expenditure. Although the R^2 value of the linear fit between foraging trip duration and total energy

expenditure (Figure 3.5a) was high at 0.88, estimated energy expenditure differed from that predicted by this relationship by an average of 19.8%, ranging from 0.1 to 60.1% (Figure 3.5b). This translates to a mean difference in energy expenditure of 20.1 kJ (range 0.1 – 95.7) over the foraging trip.

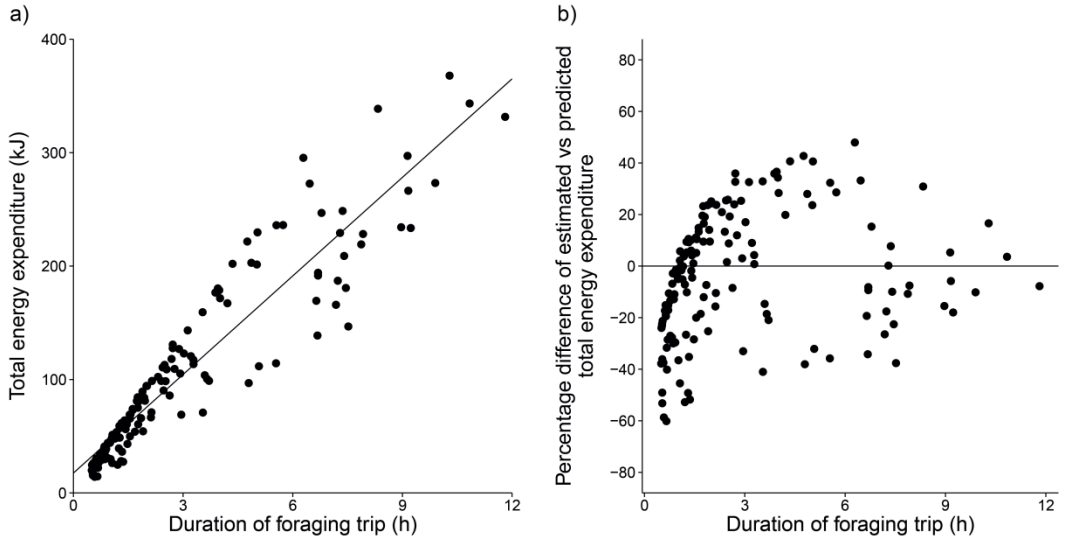

Figure 3.5. a) The relationship between foraging trip duration and total estimated energy expended during each foraging trip. The least squares regression line of best linear fit is shown. b) Difference in total measured energy expenditure as a percentage of total energy expenditure predicted from foraging trip duration using the linear relationship displayed in a).

Discussion

Activity and energy expenditure over 24 hours

Across the 24-hour day, individual kittiwakes spent the majority of time exhibiting the less energetically expensive behaviours of either attending their nest or being on the water. A greater percentage of time allocated to less energetically expensive behaviours could be due to intrinsic or extrinsic limiting factors (Humphreys *et al.* 2006; Welcker *et al.* 2009, 2010). For time spent flying to be limited intrinsically would suggest that there is a

physiological reason preventing kittiwakes from flying for more of the day, whereas extrinsic limiting factors would suggest that their behaviour was determined by an external feature such as prey availability. Both intrinsic and extrinsic factors could, and are likely to be, influencing the patterns in behaviours we recorded (Humphreys *et al.* 2006). To elucidate the causes of the potential limitations to daily activity presented, it would be ideal to combine measurements of time spent flying with indicators of rates of prey acquisition and measures of body condition. This has been achieved in two studies on chick-rearing murres, which found both an energetic ceiling determined by the ability of individuals to digest food (Elliott *et al.* 2014b), and behavioural compensation limiting DEE (Elliott *et al.* 2014a).

It is clear from our results that chick-rearing birds spend a greater proportion of time flying than do incubating birds (Figure 3.1). This increased amount of time spent flying is likely to be a result of adults needing to make regular foraging trips to provision chicks (Rishworth & Pistorius 2015). In contrast, during incubation foraging trips are less frequent due to the need for adult kittiwakes only to meet their own energy requirements (Ponchon *et al.* 2014). With flight being energetically expensive (Jodice *et al.* 2003), it stands to reason that incubating birds are more capable than chick-rearing birds of mediating their energy expenditure by flying less. Indeed, an increase in time spent flying is likely to be the most important factor in the greater DEE recorded during chick-rearing in comparison to incubation identified in many bird species (e.g. Humphreys *et al.*, 2006; Rishworth, Tremblay & Green, 2014). For kittiwakes, such an increase in energetic expenditure during this period is a likely contributor towards them having a poorer body condition, greater levels of stress, and a greater likelihood of breeding failure while chick-rearing than when incubating their eggs (Kitaysky *et al.* 1999; Ponchon *et al.* 2014). It should be noted, however, that the sample size for incubating birds in this study was much lower than that

for chick-rearing birds, thus for incubating birds the time and energy estimates must be considered with caution.

Activity and energy expenditure over foraging trips

By examining time-activity and time-energy budgets at the level of the foraging trip we have provided a more detailed level of behavioural information than has been previously available for kittiwakes. We have highlighted a large degree of variation in the relationship between trip duration and proportion of time spent flying. Although foraging trip duration correlated positively with total energy expenditure (Figure 3.5), the variation around a positive linear relationship between trip duration and energy expenditure had an average error of 19% when compared to estimates of energy expenditure which took proportion of trip spent flying into account (Figure 3.5). Notably, when looking at proportion of time spent flying plotted against duration of foraging trip (Figure 3.4) there is an absence of data points in the top right hand corner where energy costs are highest. This provides some evidence towards the presence of behavioural compensation, whereby individuals limit total energy expenditure on longer trips by spending a lower proportion of time flying. This could also be seen as providing support for the idea of an energetic ceiling, whereby individuals are constrained in their total energy expenditure at this scale (Welcker *et al.* 2010; Elliott *et al.* 2014b). This finding also highlights the inadequacy of using foraging trip duration alone as a proxy for energy expenditure. Foraging trip duration is often used as a direct indication of energy expended when away from the nest (Welcker *et al.* 2010; Rishworth *et al.* 2014), as well as an indication of foraging conditions and food availability (Kitaysky *et al.* 1999). However, we suggest that both trip duration and time spent flying should be considered together before making inferences relating to energy expenditure. Indeed, to further improve estimates of energy expenditure when away from the colony, wind conditions and time spent in either flapping or gliding flight could be considered.

Estimates of energy expenditure

The absolute DEE values we estimated for breeding kittiwakes are lower than existing published studies (Table 1). Reports of energy expenditure differ between kittiwake colonies (Table 1) and as such it may be that kittiwakes on Puffin Island are less active and expend less energy than those from other colonies. There are many possible explanations for this. For example, low intraspecific competition due to low breeding density of kittiwakes on Puffin Island could have reduced the amount of energy they needed to expend to successfully forage (Ballance *et al.* 2009), relatively short day lengths at Puffin Island compared to higher latitude colonies could limit time spent foraging, and/or the presence of the accelerometer itself may have decreased the amount of time kittiwakes spent flying (Chivers *et al.* 2016).

Table 3.1. Estimates of mean ± SD daily energy expenditure and mean body mass of chick-rearing kittiwake adults from studies published to date. All previous studies used the DLW method for estimating energy expenditure.

Study	Energy expenditure (kJ d^{-1})	Mass (g)	Location
Current study	559±19	365	Puffin Island, UK
Jodice et al. (2002)	724±171	368	Middleton Island, Alaska
Golet et al. (2000)	786±73	404	Shoup Bay, Alaska
Thomson et al. (1998)	863±177	386	Hornoya, Norway
Welcker et al. (2010)	882±88	386	Kongsfjorden, Norway
Jodice et al. (2003)	934±301	NA	Valdez, Alaska
Schultner et al. (2010)	960 ±118	377	Kongsfjorden, Svalbard
Gabrielsen et al. (1987)	992 ±273	390	Hopen Island, Svalbard
Welcker et al. (2014)	998 ±272	392	Middleton Island, Alaska

Methodological considerations may also explain our comparatively low estimates of energy expenditure. The flight model we used to estimate flight costs has been shown to

sometimes misestimate energy expenditure in comparison to empirical estimates (Mcwilliams *et al.* 2004; Schmidt-Wellenburg *et al.* 2007). The only other study providing activity-specific estimates of energy expenditure for kittiwakes, Jodice et al. (2003), suggests that flight is 5.6 times more expensive than nest attendance, whereas our approach estimates it to be 3.5 times more expensive. By following Jodice et al. (2003) and multiplying basal metabolic rate by activity-specific factors, our estimates of DEE increase to 833 ± 23 kJ d^{-1} (detailed in Appendix 3.1). Although the suitability of multiplying basal metabolic rates to estimate energy expenditure during activity is contested (Pennycuick 2008), this does indicate that low flight costs are likely driving our low energy expenditure estimates. Furthermore, the estimates of DEE we have presented have a strong linear correlation (r^2 =0.97, Appendix 3.1) with those we achieved by following the method in Jodice et al. (2003). This indicates that between these methods it is only the absolute values of energy expenditure that differ, rather than the key biological findings.

Our approach also does not take into account variation in energy expenditure relating to varying degrees of movement during behaviours. Energetic variation during behaviours may arise from sources such as switching between flapping and gliding flight, or from take-offs and landings (Shaffer et al. 2001). Amount of body movement can be quantified from acceleration data as dynamic body acceleration (DBA). DBA can be calibrated with energy expenditure either through oxygen consumption measurements in the laboratory (Halsey et al. 2009a) or with estimates from the DLW technique (Elliott *et al.*, 2013). This has been attempted for kittiwakes by Kristiansen (2014), who regressed DBA against energy expenditure as measured through the DLW technique for five birds, having discarded measurements from a sixth bird due to it being a heavy outlier. By applying the equation from their linear regression to calculations of DBA from our study birds, we estimate DEE to be 1130 ± 28 kJ d^{-1} (Appendix S3.1). Estimates of individual DEE we achieve by following this approach have a positive linear relationship with an r^2 value of 0.70 when correlated with

the estimates we have presented (Appendix 3.1). This indicates that the overall trends found using these two methods do correspond, however at the individual level, estimates of energy expenditure are variable depending on the method used. There are some serious limitations with this approach however. Firstly, a number of previous studies using DLW on seabirds have shown that estimate errors on an individual basis tend to be very large (Shaffer 2011) and as such they should not be relied upon (Butler *et al.* 2004), and in addition to this, the small sample size of the study severely limits the confidence we can have in the reported linear relationship. Furthermore, the relationship between rate of energy expenditure and DBA is not always constant across different behaviours and as such different equations for different behaviours are required to accurately estimate metabolic rate (Green *et al.* 2009; Elliott *et al.* 2013).

Estimates of energy expenditure from the current study, Jodice et al. (2003) and Kristiansen (2014) vary substantially in absolute estimates of energy expenditure, although they do all positively correlate (Appendix 3.1), thus indicating that our overall biological findings, if not the exact estimates of energy expenditure we produce, are robust regardless of method used. To identify if our low DEE estimates are due to biological or methodological reasons, detailed time-activity information is required from other colonies. The method we employ is essentially an update of traditional observation-based time-activity budgets; it is simple to implement and allows insights into variations in behaviour and their energetic consequences at a range of temporal scales and without the need for logistically demanding proxy calibrations.

Conclusion

By constructing time-activity and time-energy budgets through coupling accelerometry data with activity-specific rates of energy expenditure, we have highlighted key features of the behavioural ecology of kittiwakes as well as the deficiency of examining forage trip

duration alone when considering energy expenditure in breeding seabirds. In particular, we have provided further evidence for behavioural compensation linked to a limitation in the amount of energy individuals expend. A lack of studies using a similar method to ours has not allowed us to make a detailed comparison of DEE to that of kittiwakes at other colonies, however the relative simplicity of our approach should prompt others to employ it.

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Supplementary materials S3

Comparison of estimates of energy expenditure estimated from three different methods

Methods

To estimate energy expenditure in accordance with Jodice et al. (2003) we combined the activity-specific multiplications of BMR detailed in their study with the time-activity budgets constructed for our study birds. BMR was estimated for each individual based on their mass as per Jodice et al. using 1.197 ml CO2 g^{-1} h^{-1} (or 0.03 kJ $g^{-1}h^{-1}$). As Jodice et al. used different behavioural categories to those we used in our study, the exact values we used were derived as follows. For periods when birds were attending the nest we used their activity-specific value for nest attendance of 1.5 X BMR. For when birds were on water we combined their estimate for when birds were loafing near the colony (1.1 X BMR) and for when birds were loafing on foraging trips (4.5 X BMR). As we could not distinguish between the two behaviours in our dataset, we assumed a similar proportion of time spent in each of these behaviours for our birds as they recorded for theirs. With an estimated 21.4% of time spent loafing on foraging trips and 16.6% of the time spent loafing near the colony, we derived an estimate for when birds were on water as 3.0 X BMR. Similarly when estimating flight costs for our birds we combined the costs of commuting flight (7.2X BMR) and searching flight (6.2 X BMR) assuming 28% of the time spent searching and 21% of the time spent commuting to get an estimate of 6.67X BMR.

To estimate energy expenditure in accordance with Kristiansen (2014) required us to calculate overall dynamic body acceleration (ODBA) from our raw acceleration data. Although referred to as ODBA throughout their study, Kristiansen actually used the vectorial product of the sum of dynamic acceleration recorded by the tria-axial

accelerometer. They refer to this as $ODBA_{vec}$ in their methods section, however it is more commonly called VeDBA. We refer to it as ODBA for the sake of continuity, and made sure to follow their protocol. To estimate ODBA, as per Kristiansen (2014), we applied a running mean of 2 seconds to raw acceleration values recorded by each axis to estimate the static acceleration component ($\bar{A}$). We then subtracted this static component from the total acceleration (A) for each axis. We then converted these numbers to the absolute positive value before calculating the vectorial product as per the following equation.

$$ODBA_{vec} = \sqrt{\left(A_x - \overline{A}_x\right)^2 + \left(A_y - \overline{A}_y\right)^2 + \left(A_z - \overline{A}_z\right)^2}$$

This value gives a total of ODBAvec across the 24 hour period. As the devices used by Kristiansen, and the devices used by us were set to record at 25Hz, the values we got from their approach were directly comparable. Care should be taken to ensure this when calculating ODBA in this way.

To identify how well estimates of energy expenditure from the three methods presented (our method, Jodice et al. (2003) and Kristiansen (2014)) related to each other, we ran pairwise pearson correlations between each estimate of energy expenditure. For this we used the ggpairs function from the 'GGally' package in R 3.2.1 (R Development Core Team, 2015).

Table S3.1. Estimates of energy expenditure for each study bird based on the method presented in the current study as well as from Jodice et al. (2003) and Kristiansen (2014). Each row represents an individual bird on one day, hence repetitions under Bird ID.

			Percentage of the day spent in activity			Energy expenditure kJ d^{-1}			Energy expenditure kJ g^{-1} d^{-1}		
Bird ID	**Breeding stage**	**Mass (g)**	**Flying**	**On water**	**Nest attendance**	**Current method**	**Jodice et al. (2003)**	**Kristiansen (2014)**	**Current method**	**Jodice et al. (2003)**	**Kristiansen (2014)**
EG79073_2013	Chick-rearing	350	4	16	80	365	510	919	1.044	1.457	2.626
EG79073_2013	Chick-rearing	350	4	15	82	358	494	930	1.023	1.413	2.657
EL48309_2014	Chick-rearing	350	20	19	61	489	737	1043	1.397	2.105	2.981
EL48309_2014	Chick-rearing	350	35	19	46	596	928	1158	1.702	2.653	3.309
EL48672_2013	Chick-rearing	400	25	6	69	601	860	1209	1.502	2.149	3.022
EL48672_2013	Chick-rearing	400	37	11	52	715	1060	1196	1.787	2.650	2.990
EL48672_2013	Chick-rearing	400	40	14	47	745	1116	1288	1.863	2.789	3.220
EL48672_2013	Chick-rearing	400	35	8	57	695	1021	1321	1.738	2.552	3.302
EL48812_2014	Chick-rearing	435	25	14	61	678	975	1277	1.558	2.241	2.936
EL48855_2014	Chick-rearing	310	42	10	48	551	877	983	1.779	2.828	3.170
EL48855_2014	Chick-rearing	310	40	20	40	550	889	1309	1.774	2.866	4.223
EL48867_2013	Chick-rearing	340	24	14	61	495	750	1021	1.456	2.205	3.002
ET41812_2013	Chick-rearing	345	22	15	64	483	725	1034	1.401	2.102	2.996
EX41125_2013	Chick-rearing	330	32	17	51	534	834	1032	1.618	2.528	3.128
EX41203_2013	Chick-rearing	360	15	15	70	455	662	1035	1.265	1.840	2.876
EX41203_2013	Chick-rearing	360	24	5	71	518	754	1348	1.440	2.093	3.744
EX41211_2014	Chick-rearing	370	23	8	69	531	774	1043	1.435	2.091	2.820
EX41446_2013	Chick-rearing	350	25	19	57	520	792	1088	1.485	2.264	3.108
EX41446_2014	Chick-rearing	385	22	7	71	545	781	1095	1.416	2.029	2.844
EX41446_2014	Chick-rearing	385	28	2	70	593	853	1053	1.540	2.215	2.736
EX41446_2014	Chick-rearing	385	34	8	58	652	964	1136	1.693	2.504	2.951
EX41450_2014	Chick-rearing	350	29	26	45	562	881	1169	1.605	2.516	3.339
EY22029_2014	Chick-rearing	345	46	16	39	660	1047	1221	1.912	3.036	3.538
EY22029_2014	Chick-rearing	345	38	12	50	597	928	1307	1.731	2.689	3.788
Noring__2014	Chick-rearing	335	23	23	54	486	752	1108	1.451	2.245	3.306
EL48568_2013	Incubation	375	11	82	7	535	925	1196	1.427	2.468	3.188
EL48807_2012	Incubation	340	18	13	69	449	663	1133	1.319	1.949	3.333
EX41450_2013	Incubation	375	14	36	50	502	774	998	1.337	2.065	2.661

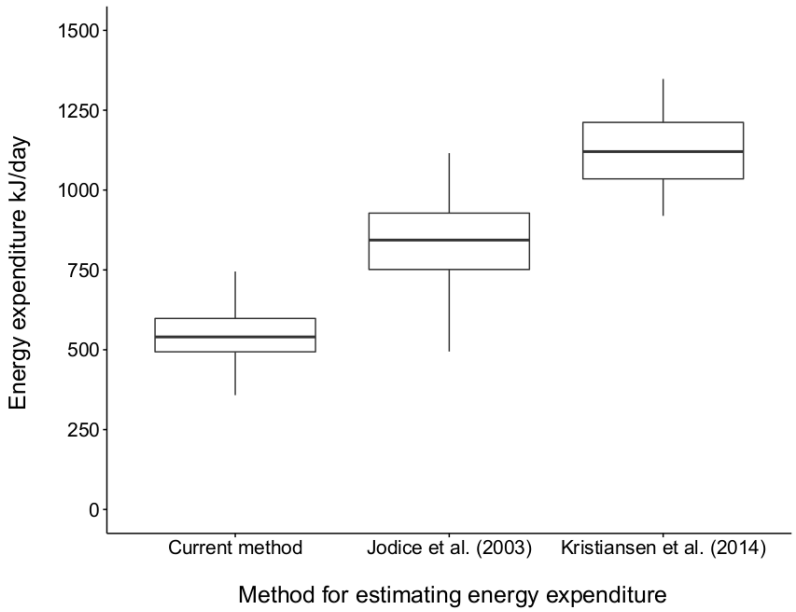

Figure S3.1. Daily energy expenditure as estimated from the current study, which applies activity-specific estimates of energy expenditure to time-activity budgets, Jodice et al. (2003), which estimates energy expenditure using activity-specific multiplications of BMR, and Kristiansen (2014), which estimates energy expenditure based on a linear regression between ODBA and energy expenditure measured via the DLW technique.

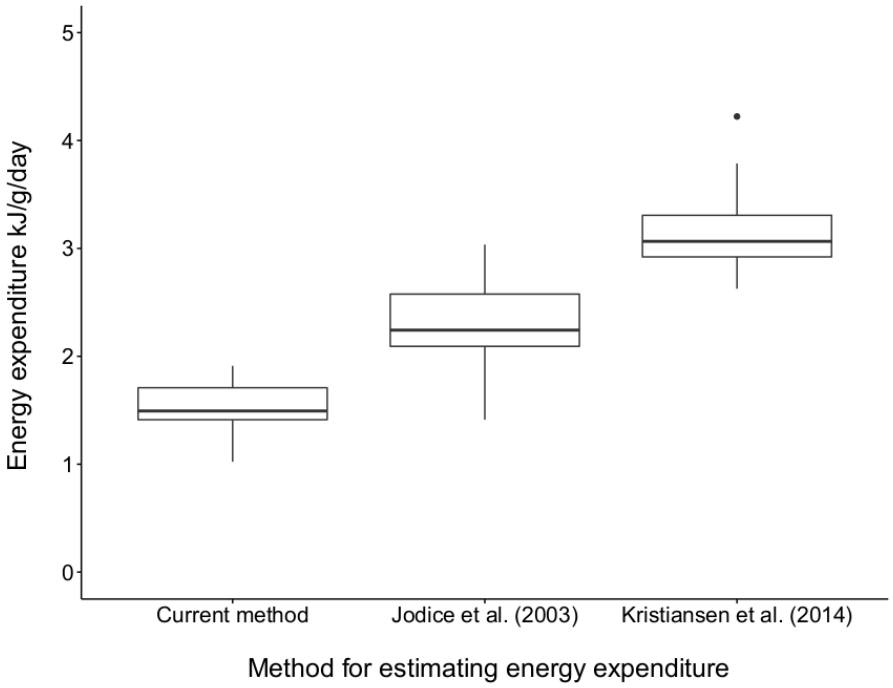

Figure S3.2. Mass-specific estimates of energy expenditure as estimated by dividing the estimates used in figure S3.1 by individual kittiwake mass (g).

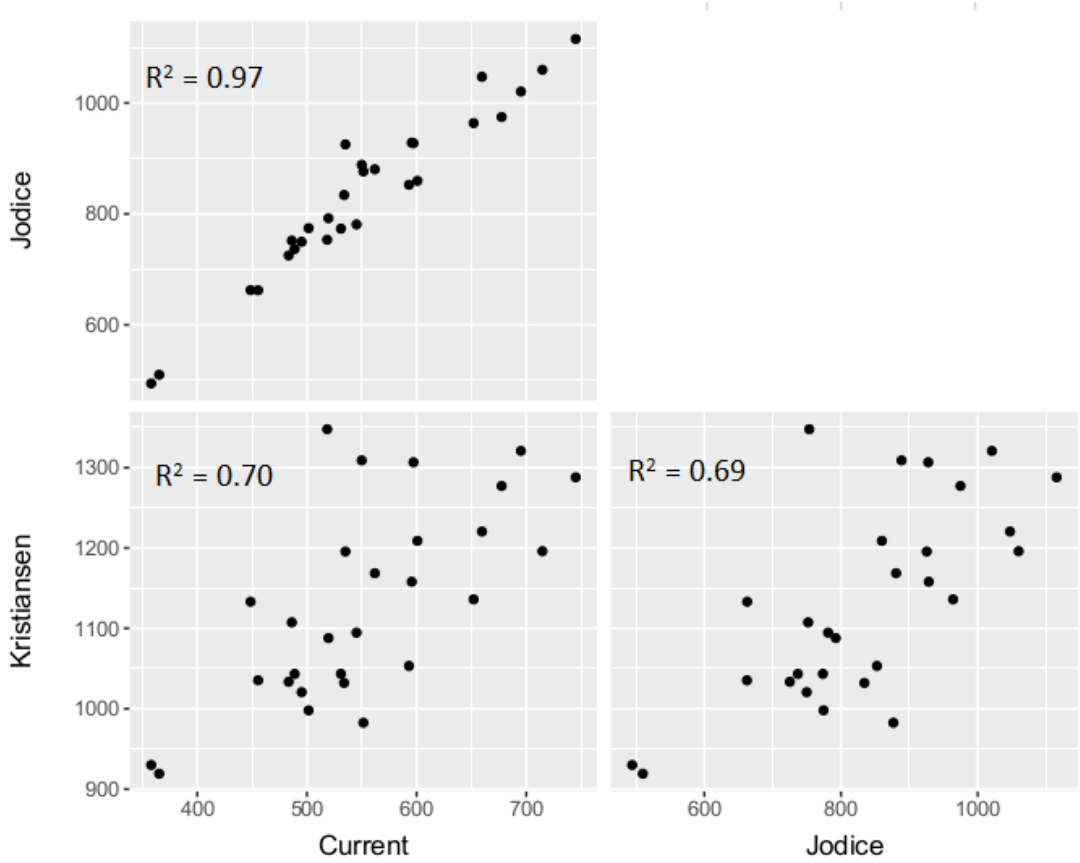

Figure S3.3. Correlations between daily energy expenditure from the three methods detailed in figure S3.1. All values are in kJ d^{-1}

Chapter 4

The journey, not the destination: How windscapes influence the flight behaviour of a breeding seabird

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Author contributions: PMC, LGH, JAG, KHE & PJAS designed the study, KHE conducted fieldwork and provided the data, PC analysed data and wrote the manuscript with support from LGH, JAG, KHE & PJAS.

Abstract

Movement is a necessary yet potentially energetically expensive process for motile animals. How individuals optimise their behaviour to take advantage of environmental conditions during movement remains poorly understood for many taxa. This is especially true for animals that move through environments where they cannot easily be observed. We examined the behaviour during commuting flights of incubating black-legged kittiwakes *Rissa tridactyla* breeding on Middleton Island, Alaska in relation to the wind conditions they face. By simultaneously deploying GPS and accelerometer devices on incubating birds we were able to quantify the timing, destination, course and speed of flights during commutes to foraging patches, as well as how wing beat frequency and strength relate to flight speeds. We found that kittiwakes did not preferentially fly in particular wind conditions, however they did increase their air speed (the speed at which they fly relative to the wind) when flying into headwinds and decrease their air speed when flying with tailwinds. This behavioural strategy maximises flight range whereby the greatest air distance is covered per unit of energy expenditure. Kittiwakes achieved greater air speeds not by flapping faster but by flapping with greater wing beat strength. A lack of influence of wind on flight destination or timing of initiation may indicate that the importance of reaching a prey patch overrides the energy expended flying in sub-optimal winds. It could also be that persistent winds over short foraging trips negate the benefit of exploiting a tailwind on an outwards flight only for it to become a headwind on the return. However, to cope with the associated energy costs likely to result from flying in sub-optimal wind conditions, kittiwakes are able to employ behavioural plasticity through adjusting flight speeds and wing beat strength.

Introduction

Energetic costs arising from locomotion can account for a large proportion of an animal's energy expenditure (Brit-Friesen *et al.* 1989). Although the way in which animals move and the energetic costs accrued through movement are largely determined by their morphology (Aerts *et al.* 2000; Dial 2003), many species exhibit behavioural adaptations to reduce their energy costs of transport. For example, great hammerhead sharks *Sphyrna mokarran* swim on their sides to exploit the greater amount of lift their abnormally large dorsal fins can then generate (Payne *et al.* 2016). Orangutans sway branches to bridge gaps in the forest canopy that they otherwise must circumvent with a route-extending detour (Thorpe *et al.* 2007; Halsey *et al.* 2016), and many ungulates nod their heads in phase with their leg movements when walking in a way that minimises the energy required to carry their head and neck (Loscher *et al.* 2016). Such behavioural plasticity to reduce costs of transport is widespread and numerous, suggesting that minimising transport energy costs is of importance (Halsey 2016).

Seabirds breed on land yet feed for extended periods of time at sea, often at great distance from their colony. They therefore face challenges associated with both environments, across varying temporal and spatial scales (Croxall *et al.* 2012). Some seabird species are exemplars of exploiting the ocean environment in a way that minimises their transport costs. Soaring seabirds with low wing loading, such as albatrosses and frigate birds, can exploit favourable wind conditions to travel vast distances while expending very little energy (Shaffer 2011). This shapes not just the way in which they fly, but also where they choose to fly (Weimerskirch *et al.* 2000, 2016). Indeed, the foraging areas of albatrosses have changed over time to match shifts in prevailing wind conditions (Weimerskirch *et al.* 2012). At the other extreme, species such as murres and shags that have a high wing loading and need to continuously flap to stay in flight, face exceptionally high flight costs

(Elliott *et al.* 2013a; b) that can be exacerbated by strong winds (Elliott *et al.* 2014). The flight costs for these birds are perhaps so high because they are approaching the functional boundary between flight and non-flight due to their wings being optimised for diving performance (Elliott *et al.* 2013a).

The breeding season is a suitable period in which to study the influence of extrinsic parameters on the movement behaviour of seabirds. Being central place breeders, seabirds not only have to deal with the direct energetic costs associated with raising young (Regular *et al.* 2014), but also with the time and energy costs of frequently commuting between their breeding site and foraging grounds. Although this constraint limits the at-sea areas they can exploit, foraging behaviour during the breeding period can be highly variable both within and between populations (Kotzerka *et al.* 2009; Soanes *et al.* 2013, 2014). How individuals respond to prevailing wind conditions during this period of high energy demand hampered by time-constrained movement (Gales & Green 1990; Shaffer 2004) is poorly understood for most seabird species. This is largely due to flight being particularly difficult to study in-situ (Elliott 2016). Theoretical approaches to understanding flight have led to aerodynamic models being developed to predict how individuals might fly in a way that minimises the costs of transport. Two different speeds have been proposed to explain how continuously flapping birds might adjust their flight: maximum range speed and minimum power speed. Maximum range speed is the speed that covers the greatest air distance per unit of energy, while minimum power speed is the speed corresponding to the lowest required energy expenditure to stay in flight. Minimum flight speed leads to the longest time spent flying without needing to refuel, yet doesn't result in the greatest distance travelled before needing to refuel (Pennycuick 2008). According to optimal flight theory, maximum range speeds are predicted to increase when flying into headwinds, while

minimum power speed is not affected by wind speed (Hedenström & Alerstam 1995; Hedenström *et al.* 2002).

Biologging devices can be used to study flight in-situ by continuously recording both the location of individuals and the movement of their bodies. These devices can shed light on the movement choices and flight behaviours of birds at sea (Cooke *et al.* 2004), allowing us to investigate whether they do indeed optimise their flight in line with theoretical models. To date, studies using biologging devices to examine the influence of wind on seabird flight have tended to focus on the extreme soarers such as frigate birds and albatrosses (eg Wakefield *et al.* 2013; Weimerskirch *et al.* 2016) or, at the other end of the spectrum, species with obligate flapping flight such as shags (e.g. Kogure et al. 2016). Less is understood about how birds with more flexible flight behaviours, which represent the majority of species, either utilise and/or are constrained by wind conditions. Here we focus on the studying the flight behaviour of the black-legged kittiwake *Rissa tridactyla* (hereafter kittiwake). The kittiwake is a medium-sized species of gull which feeds at, or slightly-below, the sea surface. Being incapable of actively pursuing prey through the water column, flight is its single mode of locomotion when travelling at sea. Kittiwakes have a flap-glide style of flight, though for the vast majority of time exhibit flapping flight (Brit-Friesen *et al.* 1989). Flight costs account for a large proportion of the energy expenditure of breeding kittiwakes (Collins *et al.* 2016). We therefore predict that birds such as kittiwakes should make judicious use of their energy stores during foraging trips, yet we do not know the scales at which these decisions might operate. In the present study we aim to bridge this knowledge gap, elucidating how kittiwakes respond to wind conditions during commuting flights that form part of foraging trips. By combining simultaneous GPS and acceleration data with measures of wind speed and direction, we examine the flight behaviour at two scales of adjustment. At a broader scale we ask the question: How does wind influence destination

and timing of commuting flight? While at a finer scale of adjustment we ask the question: How do kittiwakes alter their flight speeds and wingbeat patterns in response to wind conditions? Both of these questions are addressed with the aim of identifying evidence of behavioural strategies for coping with the time and energy constraints breeding individuals face.

Methods

Data collection

We collected simultaneous GPS and tri-axial accelerometry data from 62 incubating kittiwakes breeding on the radar tower colony on Middleton Island, Alaska (59°27'N, 146°18'W) between May 30 and June 18 2013. Accelerometers (3 g, Axy, Technosmart, Rome, Italy) were set to record at 25 Hz, while GPS loggers (14 g, CatTraQ™, Catnip Technologies, USA) were set to record at 1 minute intervals. Both devices were attached (as a single combined unit) to the central back feathers of kittiwakes using strips of TESA tape. Data was collected from 62 birds, however we used only those which successfully recorded both accelerometry and GPS data simultaneously, and which recorded data until retrieval of the loggers, thus giving a dataset of 47 combined deployments. The mean kittiwake mass at time of deployment was 467±37 g (range 395-540 g). The GPS and accelerometer combined weighed a total of ~ 20 g when packaged, thus accounting for a mean of 4.3% of body mass (range 3.7-5.1%). Devices of an equivalent mass have been shown to reduce the amount of time kittiwakes spend flying, although no effects on longer term performance measures such as reproductive success were detected (Chivers *et al.* 2016). The device effect on behaviour needs to be considered when interpreting the results, however instrumented birds still needed to (and indeed did) fly when carrying

biologgers and as such we suggest that the overall influence of wind on movement behaviour was likely to remain.

We used a weather dataset from the Middleton Island Airport that comprised of wind speed and wind direction recorded within 1 km of the colony at 20 min intervals (http://cdo.ncdc.noaa.gov/qclcd/QCLCD). We collated these data from the start time of the first logger dataset to the end of the last. To characterise the overall prevailing wind conditions and to identify if there was an association between time of day and wind conditions, average wind speed and direction per hour of the day were calculated and visualised using the "metvurst" package in R 3.2.1 (R Core Team 2015).

Behavioural assignments

To identify periods of flight and full foraging trips, acceleration data were assigned to three coarse-scale behaviours: "nest attendance", "on water", and "flying". Although finer-scale behaviours such as foraging, preening, and courtship are exhibited by kittiwakes, the amount of time these behaviours take up is relatively little (Jodice *et al.* 2003). As per Collins et al. (2015), behaviours were assigned using a simple method that categorises different activity types based on readily calculable metrics indicating body orientation or amount of movement. Behaviours of "nest attendance" and "on water" were assigned depending on the body angle of the bird; periods when the bird was at a lower angle were assigned as "on water", and periods at which the bird was at a higher body angle were identified as being on land. The body angle thresholds at which these behaviours were separated were specific to each individual. When classified as on land, birds were assumed to be attending their nest, and were thus assigned the behaviour "nest attendance". Flight was assigned based on the standard deviation of acceleration values in the heave axis, with higher values indicating movement in this channel relating to flight. This method of

behavioural classification has been shown to give high accuracy (>95%) of coarse-scale behaviour assignments in kittiwakes (Collins *et al.* 2015). However, to further enhance the accuracy of this approach, a rule was applied to the data whereby assignments of "on land" could not be assigned when accompanying GPS data indicated that the bird was at sea; likewise when GPS data indicated that the bird was over land an assignment of "on water" could not be made. Foraging trips were defined as a period in which the bird flew from the land, spent time on water, and then returned to the land, with trips varying in duration. Only trips over 30 min were used, to exclude periods when birds might have left the land for reasons other than foraging (such as researcher disturbance or predator avoidance (Collins *et al.* 2014)). Flight was not separated into flapping or gliding, although kittiwakes flap much more than they glide (Brit-Friesen *et al.* 1989), as verified by visual examination of the raw heave axis acceleration data.

Spatial analysis

As per Warwick-Evans *et al* (2015) we interpolated GPS tracks to one fix per second using the "adehabitatLT" package (Calenge 2006) in R 3.2.1 (R Core Team 2015) so that it was at the same frequency as, and could therefore be combined with, accelerometry behaviour data. We used the "geosphere" package in R (Hijmans *et al.* 2016) to measure the distance between interpolated GPS locations to calculate total distance travelled and maximum distance from the colony.

Kernel density analysis

We used the Geospatial Modelling Environment software (Beyer 2012) to estimate the kernel densities and the 50% kernel home ranges of the birds' at-sea distributions. Only data relating to when birds were in flight (as indicated by prior behavioural assignments) were included in the distribution density estimates. This analysis therefore reflects foraging

destinations and flight directions, rather than areas where the birds may have spent a large amount of time loafing on the water. Cell size was set to 1 km^2 while the bandwidth was obtained using the plug-in estimator (Wand & Jones 1994) in the "ks" package (Duong 2015) in R.

Flight speeds and direction

GPS data were used to calculate measures of flight speed per second. The ground speed vector $\mathbf{V_g}$ (the speed of flight measured from the GPS track) was calculated by dividing measured distance travelled by time taken, while the air speed vector $\mathbf{V_a}$ (the speed the bird is flying after accounting for the speed and direction of the wind) was measured by subtracting the wind speed vector in direction of travel $\mathbf{V_w}$ from ground speed (Kogure *et al.* 2016):

$$\mathbf{V_a} = \mathbf{V_g} - \mathbf{V_w}$$

The wind speed vectors were calculated by estimating the wind vector in direction of flight using the "RNCEP" package (Kemp *et al.* 2012) in R. All speeds were calculated in m s^{-1}. Although ground and air speeds were calculated for all flights, we excluded from our analyses flights relating to periods when the birds were most likely foraging - identified through measures of speed estimated in R and visual inspection of the data in ArcGIS (ESRI, USA, version 10.0) as having high tortuosity and low ground speeds. Foraging was omitted so that we could focus on the influence of wind on flight and movement without the potential confound of behavioural decisions relating to searching behaviours. Flight speeds used in analyses are averages across each flight, with the first and last 50 seconds removed to reduce the influence of take-off and landing changes in speed.

Flight direction was examined at two scales. To understand the general direction of travel for first and last commuting flights in a foraging trip, the direction between the first (take-

off) and last (landing) GPS fixes of these flights were calculated. Whereas to identify if birds preferentially flew with wind assistance when in flight, the angular difference between the direction of flight and wind direction during flight was calculated. Direction of flight was subtracted from wind direction per second during each flight and then averaged across each full flight. By calculating this value per second we account for potential changes in both wind and bird direction during flights. To identify if there was any significant deviation from a uniform distribution of angular differences between flight and wind directions we conducted a Rao's spacing test (alpha = 0.05).

Wing beat parameters

Dominant wing beat frequency was calculated using peak spectral density on Fast-Fourier transformed acceleration values in the heave axis (the dorso-ventrally orientated axis). It was calculated across commuting flights, however the first and last 50 s of each flight was removed due to wing beat frequencies being more variable during take-off and landing (Elliott *et al.* 2014). As per Kogure *et al* (2016), wing beat strength was calculated using the Ethographer application (Sakamoto *et al.* 2009) in IGOR Pro (Wavemetrics inc., USA 2008, Version 6.37). Continuous wavelet transformation was applied to the raw acceleration data in the heave axis, and wing beat strength was calculated as the average of absolute amplitude of each waveform every second. As with estimates of wing beat frequency, the values we derived relate to the dominant wing beat strength across each commuting flight period, with the first and last 50 s of each flight removed.

Statistical analysis

All inferential statistical analyses presented relate to values derived across individual flights. Only flights of a duration of more than 5 min were included in the analyses to ensure that the dominant wingbeat frequency and dominant wingbeat strength

measurements were more likely to represent the dominant signal rather than an outlying value from highly variable signals.

A series of generalised linear mixed models (GLMMs) were constructed to test for the influence of wind on various aspects of flight behaviour. GLMMs were constructed for both flight duration and total distance travelled in relation to wind speed and direction. Further GLMMs were then constructed to examine the influence of the wind speed component in the direction of travel (hereafter tailwind speed) on estimated ground and air speeds across flights. Following Shamoun-Baranes et al. (2007), and as implemented by Yoda et al. (2012) and Kogure et al. (2016), we also applied a two-dimensional GAM to analyse the relationship between air speed and wind speed during flights. Wind speed was separated into two components - headwind speed and crosswind speed - and was transformed via LOESS transformation (with a maximum span of 80% and 2 degrees of freedom). Analysis was conducted in the "mgcv" package (Wood 2001) in R. This additional analysis was carried out to identify if findings from the GLMMs were likely to be spurious correlations that can arise from analysing wind data with a one-dimensional model (Shamoun-Baranes *et al.* 2007). We also constructed GLMMs to identify how air speed was related to the dominant wing beat frequency and wing beat strength for individual flights. Due to each kittiwake undertaking numerous flights during the period in which they were measured, individual bird identity was assigned as a random factor in all GLMMs. All GLMMs were constructed with a Gaussian family and a log link due to each response variable conforming to assumptions of normality. GLMMs were constructed using 'glmmPQL' from the MASS package (Venables & Ripley 2002) in R. P values below 0.05 were deemed to be statistically significant.

Results

Broad-scale behaviour

Distribution and direction of flights

We detected a total of 107 foraging trips, which included a total of 558 discrete flights with a duration of 5 min or more. On average, foraging trips included 5.2±0.5 discrete flights (range 1 – 26) separated by either feeding bouts or periods of resting on the water. In total, 402 of these flights were classified as commuting flights, thus fitting the criteria for subsequent analysis. Mean duration of these flights was 12.1±0.68 min, covering a mean distance of 5.18±0.41 km. Mean foraging trip duration was 4.3±0.4 h (n=77), with mean percentage of total time spent in flight throughout a foraging trip being 47.3±2.5%. The mean total distance travelled per foraging trip was 73.3±5.1 km (range 10.7-201.9 km), with the mean maximum distance from the colony being 21.6±1.4 km (range 3.0 – 57.6 km).

The majority of recorded foraging trips were to the north, or slightly northeast, of the colony (Figure 4.1). The 50% kernel density estimates for space use when on a foraging trip highlight the importance of the area immediately to the North of Middleton Island (Figure 4.1). 94% of initial flights headed northwards between 315 - 135°, whilst 87% of final flights in each foraging trip (i.e. the return trips) headed southwards, between 135-270° (Figure 4.2).

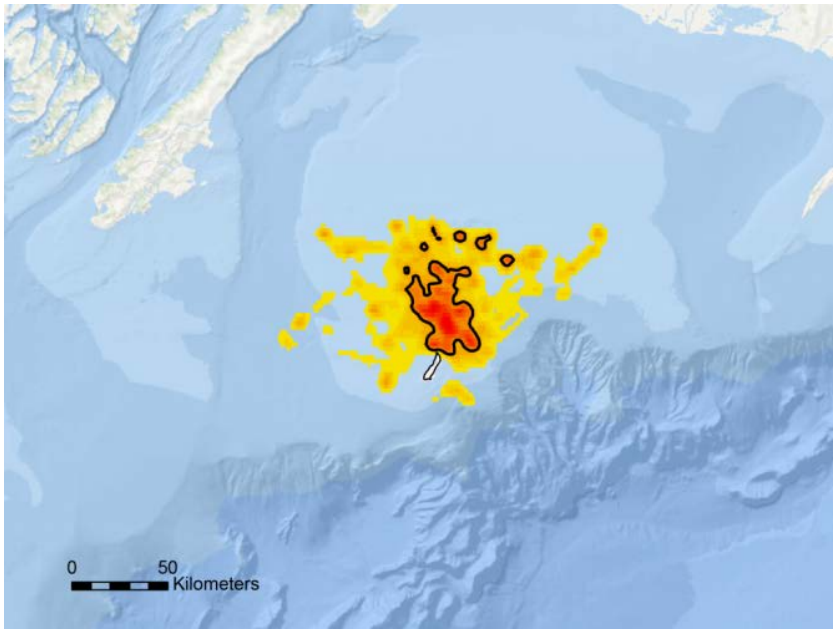

Figure 4.1. Kernel density for the distribution of all foraging trips across the study period. The intensity of the yellow to red colours indicates density of GPS fixes, with the darker red indicating higher density. The solid black line surrounding the red represents the 50% kernel estimates. Middleton Island is the white shape central to the image, just below the 50% kernel outline.

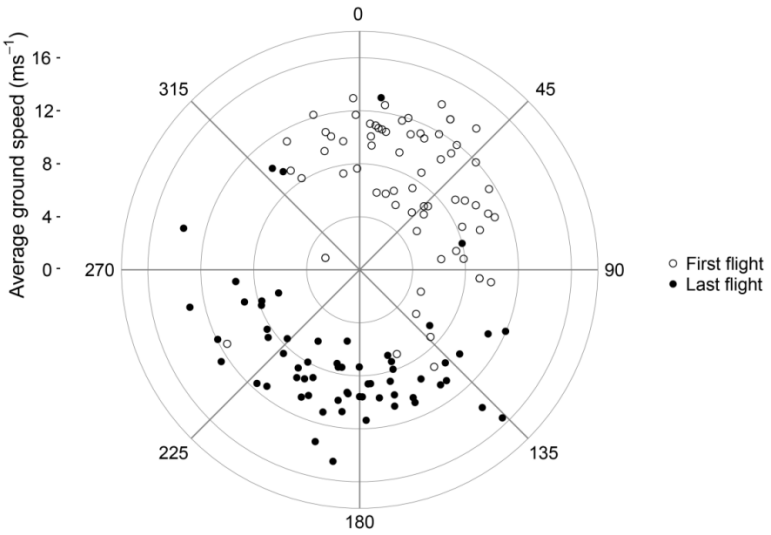

Figure 4.2. Direction flying towards, and average ground speed of, the first and last flight for each foraging trip.

The influence of wind on initiation and direction of flights

Throughout the study period winds tended to come from either a south to south westerly direction (200-270°) or from a north-easterly to easterly direction (40-100°). Mean wind speed was 4.2±0.1 m s^{-1} (range=0-11.2 m s^{-1}). There was no diurnal pattern in wind direction or wind speed (Figure 4.3).

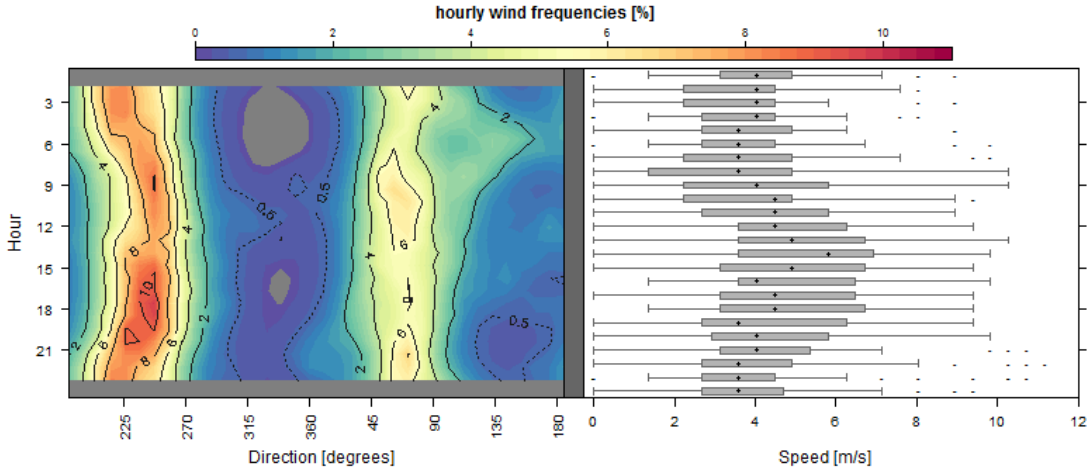

Figure 4.3. Wind contours for the full duration of the study. The left hand panel indicates hourly frequencies of wind direction, while the panel on the right indicates the distribution of wind speeds per hour. Note that charts indicate the direction wind is coming from.

Hourly wind direction weighted by the number of birds equipped during each hour, and thus indicating available wind conditions for study birds to fly in, reflected the dominant wind conditions over the study period, with winds blowing from either a south to westerly direction or a north east to easterly direction (Figure 4.4a).

Birds showed no clear preference for flying during periods when the wind was blowing from certain directions or at certain speeds. The distribution of wind conditions during: all flights (Figure 4.4b), the first flight of each foraging trip (Figure 4.4c) and the last flight for each foraging trip (Figure 4.4d) did not differ from the overall wind conditions during the study period (Figure 4.4a). Flight duration was not significantly related to either wind

direction (t_{357}=-0.67, p=0.503) or wind speed (t_{357}=-1.37, p=0.172), however total distance travelled during a flight was significantly greater with lower overall wind speed (t_{357}=-2.78, p=0.006), but was not significantly related to overall wind direction (t_{357}=-0.67, p=0.503).

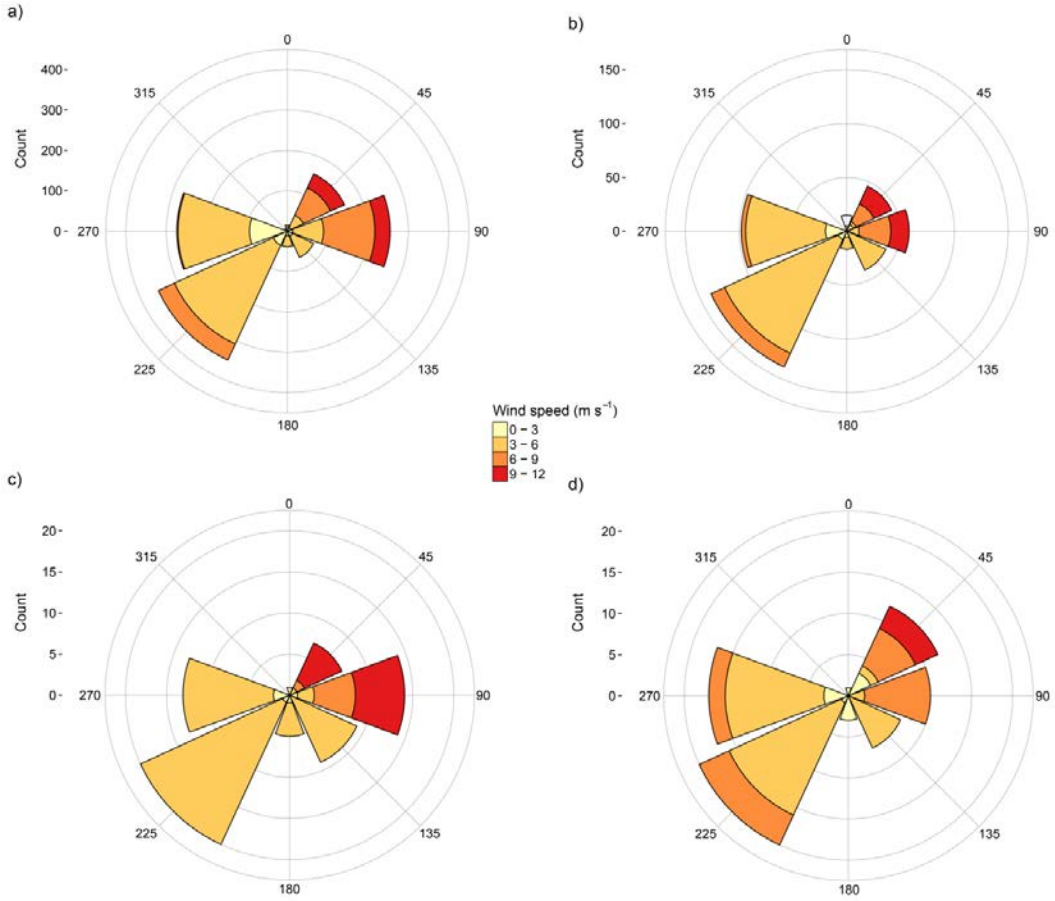

Figure 4.4 – Wind rose diagrams showing wind direction and strength for: a) the full study period weighted by sample size, b) all flights, c) the first flight from each foraging trip, d) the last flight from each foraging trip. Note that charts indicate the direction wind is coming from.

There was no evidence of birds preferentially flying with tail winds when in flight. The angular difference between wind direction and the overall direction the bird flew in during each flight showed no significant deviation from a uniform distribution (Rao's spacing test,

U=136, p>0.05). Wind speed also did not appear to influence the direction the bird was travelling in relation to the wind (Figure 4.5).

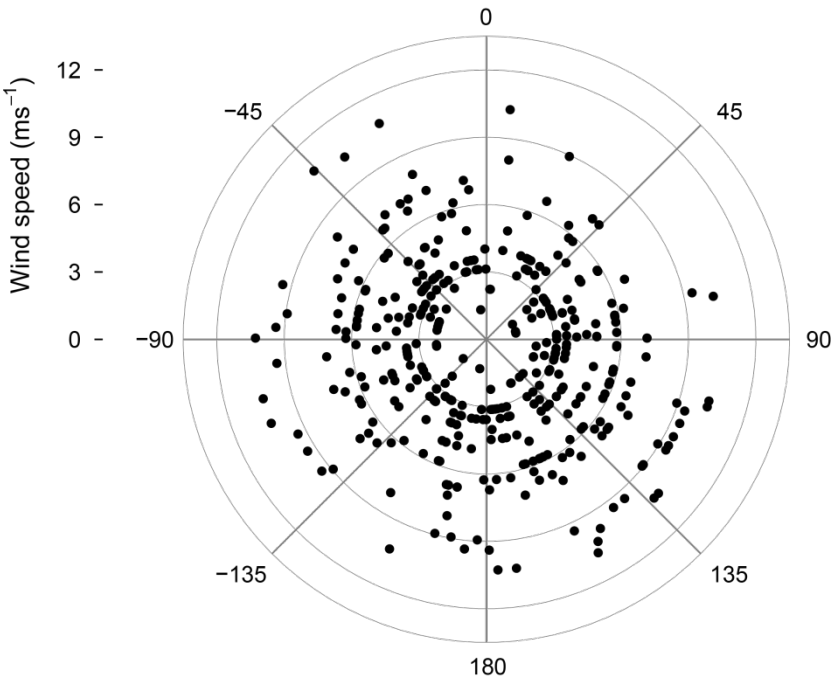

Figure 4.5 The angular difference between flight direction and wind direction for all flights. Each black dot represents a flight, values closer to 0 represent birds flying with a tailwind, whereas values of 180 indicate flights in which birds were flying with a headwind.

Fine-scale behaviour

The influence of wind on flight speed and behaviour

Wind speed and direction relative to the birds influenced their speed of travel. Ground speed increased significantly with tailwind speed, described as: ground speed=8.38+0.34*tailwind speed (Figure 4.6a) (t_{382}=8.62, p<0.001).

Air speed significantly decreased with increasing tailwind speed (t_{378}=-18.57, p<0.001), described as: air speed=9.69-0.60*tailwind speed (Figure 4.6b). A two- dimensional GAM identified that air speed was significantly related to one or both of the wind components (tailwind and crosswind) in all individuals (P<0.001), suggesting the relationship is not due to a spurious correlation.

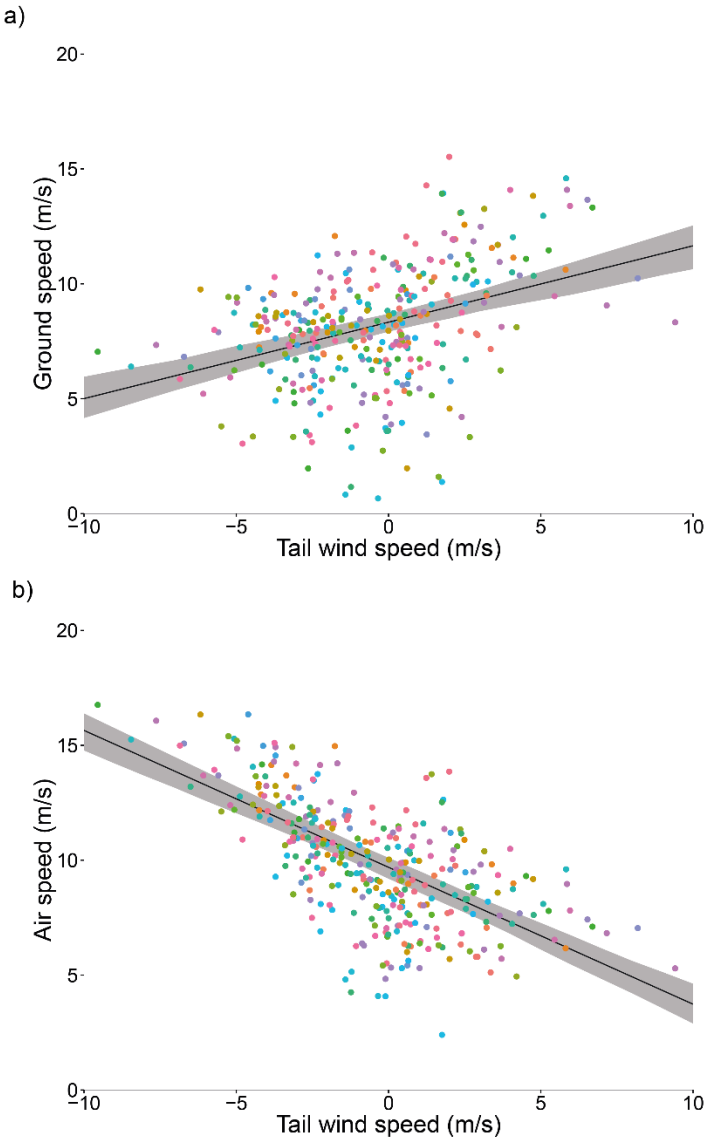

Figure 4.6. The relationship between tailwind and a) air speed; b) ground speed for all flights over 2 min. Each colour represents an individual bird. The solid line indicates the fixed effect relationship, with the grey ribbon indicating the 95% confidence intervals.

Wing beat strength significantly increased with increasing air speed (t_{378} = 5.23, p<0.001) (Figure 4.7a) whereas there was no significant relationship between wing beat frequency and air speed (t_{378} = 1.41, p=0.160) (Figure 4.7b). Mean wing beat frequency across all flights for all individuals was 4.07±0.01 Hz (range= 3.57-4.85).

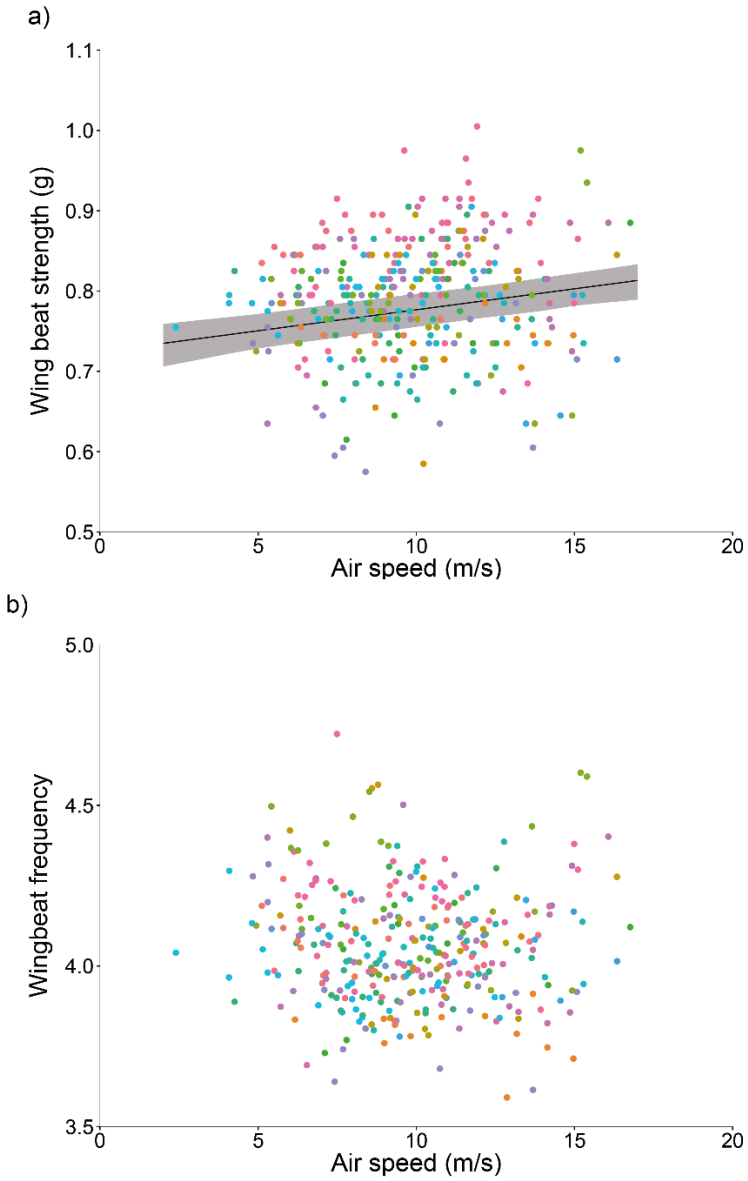

Figure 4.7. The relationship between air speed and a) wing beat strength and b) wing beat frequency for all commuting flights. Each colour represents an individual bird. The solid line indicates the fixed effect relationship, with the grey ribbon indicating the 95% confidence intervals.

Discussion

By coupling positional data with body acceleration and windscape data we have cast some light on the complex interaction between movement behaviour, energetic costs and extrinsic influences in a commuting seabird. We found that these birds select the location, timing and course of their commuting flights apparently without consideration of the strength and direction of winds they experienced. This suggests that, for this population at least, extrinsic factors other than wind are more important in determining initiation and destination of flights. However, once in flight kittiwakes do modulate their behaviour by increasing flight effort in the face of headwinds and reducing effort when being assisted by tailwinds. This further demonstrates the capacity for animals to make proximate adjustments to their behaviour to optimise the costly investments in transport energy use.

Broad-scale behaviour

This consistency of foraging trip destination and flight direction of kittiwakes to and from Middleton Island (Figures 4.1 & 4.2) indicates that they may be exploiting a reliable food source. As we do not have prey density data for the area surrounding the study colony we cannot confirm this supposition. However, the association of foraging destination with areas of high prey availability has been demonstrated in many seabird species (Fauchald & Erikstad 2002; Weimerskirch 2007; Burke & Montevecchi 2009; Raymond *et al.* 2010). Despite this consistent foraging destination, kittiwakes did not display a preference for initiating commuting flights during tailwinds (Figures 4b-4d). Preference for flying in favourable conditions has been shown during migratory flights in various groups of birds, including passerines, raptors and seabirds (Åkesson & Hedenström 2000; Liechti 2006; Mateos-Rodriguez & Bruderer 2012). There has also been some indication that soaring seabirds leave their nests to forage more frequently during stronger winds, when they

would benefit from wind assistance (Furness & Bryant 1996). A lack of preference exhibited by the kittiwakes of Middleton Island could relate in part to the study birds being at the incubation stage of breeding. Kittiwakes sharing egg incubation are obliged to keep foraging trips short (mean trip duration in this study was 4.3±0.4 h) and thus the prevailing winds, which tend to persist for a number of hours (Figure 4.3) are unlikely to have changed between their outward and return journey. Given the kittiwakes of Middleton Island typically return to the colony from the direction in which they headed out in (Figure 4.2), a favourable tailwind on the outward journey is therefore an unfavourable headwind during the return and so there may be little to gain from waiting for a favourable tailwind for departure. This is especially true if flying in a strong headwind is energetically more expensive than flying in a strong tailwind is beneficial.

As well as not adjusting timings of flights, we also found that the kittiwakes did not appear to adjust their direction of flight in relation to the wind (Figure 4.5). This is in contrast to species such as albatrosses and red-footed boobies, which show behavioural adjustment of flight paths to ensure they minimise the proportion of the time they fly into headwinds (Weimerskirch *et al.* 2005; Wakefield *et al.* 2013).

It could be that recorded wind conditions did not reach sufficient strength to either blow kittiwakes off course or influence their decisions off when and where to fly during commuting flights. Wind conditions during the study period did not consist of prolonged periods of high winds (Figures 4.3 and 4.4); average wind speed over the study period was 4.2±0.1 m s^{-1}. This is similar to the average wind speeds across the full breeding period, (between March and September) which averaged 4.8±2.8 m s^{-1}, although there is monthly variation in recorded wind speeds, with winds tending to be weaker in the months of June and July. Furthermore, wind direction was overall quite consistent throughout the study

period, and it might be that comparisons of flight behaviour during periods of more contrasting wind conditions, or even a comparison with flight behaviour with kittiwakes from colonies experiencing different wind conditions could further elucidate the influence wind speed and direction has on initiation and direction of flight for breeding kittiwakes.

Evidence for the influence of the windscape on most foraging seabirds is scarce, however moderate winds speeds (mean = 2.7±1.4 m s^{-1}) have been shown to not alter foraging location in great cormorants (mean wind speeds of 2.7±1.4 m s^{-1} in Yoda *et al.* 2012), while wind speed and direction seemed to have an inconsistent influence on direction of flight for common murres *Uria aalge* (Davoren *et al.* 2003). Strong winds, however, have been shown to reduce foraging behaviours and change flight behaviours in other species such as European shags (Daunt *et al.* 2005). It is worth noting, however that these species all have higher flight costs than do kittiwakes (Masden *et al.* 2010).

The consistency of foraging destination, absence of selection towards flying during favourable wind conditions, and the lack of adjustment of flight course in response to wind speed and direction suggest that wind was not a sufficient extrinsic factor in shaping the commuting flight behaviour of kittiwakes in this study. It is likely that prey availability, or perhaps time constraints requiring kittiwakes to reach prey quickly, superseded wind speed and direction in determining the broader-scale features of commuting flight in this study.

Fine-scale behaviour

Flight speeds

The prevailing wind conditions did influence the flight speeds and flapping behaviour of kittiwakes. An increase in headwind decreases their ground speed but increases their air speed, while an increase in tailwind increases their ground speed but reduces air speed (Figure 4.6). This fits with the idea that birds are adjusting their flight speeds to fly towards

a maximum range air speed, whereby the greatest air distance is covered per unit of energy consumed (Pennycuick 2008; Kogure *et al.* 2016; Mclaren *et al.* 2016). This finding of adjusting air speed to fly faster in headwinds and slower in tail winds is consistent with findings from previous studies on kittiwakes (Elliott *et al.* 2014) and a host of other seabird species (Shamoun-Baranes & van Loon 2006; Mateos-Rodriguez & Bruderer 2012; Kogure *et al.* 2016).

Wing beat patterns

The positive correlation between headwind speed and air speed indicates that kittiwakes worked harder in headwinds than they did in tailwinds, and therefore expended more energy per unit time when flying into the wind. Although Elliott et al. (2014) reported a positive correlation between air speed and wing beat frequency our findings suggest that kittiwakes instead increase their air speed through wing beat strength. Our study differed from Elliot et al (2014) in many ways. Primarily we analysed commuting flights at all stages of foraging trips, rather than only inbound or outbound flights. Furthermore, rather than averaging across all inbound or outbound flights we recorded the relationship between air speed and wing beat strength within each flight. In accordance with our findings, adjustment of air speed through moderating wing beat strength has been noted in European shags *Phalacrocorax aristotelis* (Kogure *et al.* 2016). Other species such as bar-headed geese have been recorded to control flight effort and flight speeds through wing beat frequency (Schmaljohann & Liechti 2009; Bishop *et al.* 2015). This highlights that different species control their flight effort through varying nuances of wing movement.

Optimising energy expenditure

Although animals show adaptations towards reducing energy expenditure during locomotion, it is unlikely that they are consistently travelling in the most energetically

efficient way (Halsey 2016). Other pressures such as time-constraints to relieve an incubating partner (Chaurand & Weimerskirch 1994) or predation threats to chicks (Thometz *et al.* 2016) are likely to influence the movements of central place foragers such as kittiwakes. Whether individuals are able to predict or identify the most energetically efficient method of locomotion is not well understood. Shamoun-Baranes *et al.* (2016) found that on return flights to their colony, gulls do not exploit the most energy efficient path of flight, perhaps because they are unable to predict it. A similar result has also been described for foraging gannets (Amélineau *et al.* 2014). For the kittiwakes in this study, time constraints from relieving an incubating partner and/or an inability to identify or wait for optimal flight conditions could be responsible for the patterns we observed. Furthermore, as kittiwakes tend to fly for a lower proportion of their time during incubation than during the chick-rearing period (Collins *et al.* 2016), it may be that optimising flight behaviour to reduce energy costs returns little benefit during this time.

Flight costs tend to be asymmetrical, whereby the costs of flying into a headwind outweigh the benefits of flying with the equivalent tailwind (Raymond *et al.* 2010). This may be of fundamental importance to the flight behaviours of foraging birds that display directed flight to and from a foraging destination during their breeding season. Waiting for a favourable tailwind will not be beneficial and indeed this appears to be the case with further interrogation of the data presented here. By calculating the time required to cover a set distance of 5 km under varying wind speeds given the flight speeds we measured (Figure 4.6) we can empirically show that headwinds are more unfavourable than tailwinds are favourable. The asymmetrical shape of the relationship between time taken to cover 5 km and tailwind speed indicates that it takes an increasing amount of time to cover a distance as tailwinds become headwinds (Figure 4.8). Furthermore, when flying into

headwinds not only will kittiwakes be flying for longer, but they will be flapping just as frequently but with a greater wing beat strength, thus expending more energy.

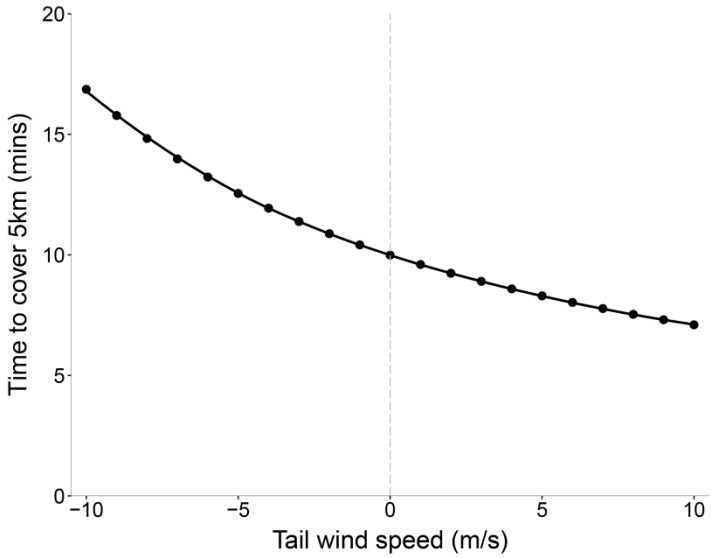

Figure 4.8. The time taken for kittiwakes from Middleton Island to travel 5 km over the ground in a straight line dependent on wind speed. Positive values along the x-axis indicate tail winds in relation to the bird, whereas negative values indicate a headwind. Times were calculated from the relationship between ground speed and tailwind described in Figure 4.6a. The curved line is a smoothed conditional mean, calculated using a LOESS estimator.

Conclusion

Middleton Island kittiwakes seem unperturbed by the wind conditions they experience when commuting to and from foraging patches. Perhaps the additional energy costs of unfavourable winds are negligible or unimportant, or perhaps waiting for better conditions is outweighed by the time lost to not feeding at reliable foraging sites. Another possibility is that persistent winds and relatively short foraging trips mean the same wind conditions will be experienced both on the outward and return journeys, nullifying, or even reducing the value of tailwinds on one leg of the trip or the other. However, once in flight the birds

respond to wind conditions by adjusting the pattern of their wing beats to take maximal advantage of tailwinds and minimise the impact of headwinds, thus optimising the speeds at which they fly. Thus wind speed and direction are not the major extrinsic factors determining the broad-scale flight behaviour of kittiwakes. While the windscape impacts their overall energy costs, through plasticity in flight speeds and wing beat patterns kittiwakes can minimise this expense.

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Chapter 5

Predation of black-legged kittiwake chicks *Rissa tridactyla* by a peregrine falcon *Falco peregrinus*: Insights from time-lapse cameras

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Abstract

We directly recorded predation of Black-legged Kittiwake chicks *Rissa tridactyla* by a Peregrine Falcon *Falco peregrinus* using a remote time-lapse camera. Between 20 July 2013 and 23 July 2013 all four nests in the camera's field of view failed. A Peregrine was recorded predating chicks in two of these four nests. Periods of adult desertion at the other two nests strongly suggests chicks in these nests were predated as well. Predation happened at night, a rarely documented behaviour of the peregrine falcon. Along with giving insights in to peregrine falcon hunting behaviour, the use of remote cameras allows us to determine nest fate. Determining sources of chick mortality is valuable for identifying causes of variability in productivity rates of colonial breeding birds.

Nest predation is a major selection pressure in all bird species, influencing a range of life-history traits (Martin 1995) . In the absence of ground predators, avian predation can be an important source of breeding failure in colonies of cliff nesting seabirds (Clode 1993). However the short lived nature of predation events makes them difficult to observe in conjunction with standard seabird monitoring protocols, which typically involve making visual observations intermittently at optimum stages throughout the breeding season (Walsh *et al.* 1995). This leads to predation not always being sufficiently considered as a source of mortality when assessing factors influencing colony productivity. By properly measuring predation, the potential bias of attributing nest failure to other factors such as food shortage or environmental change can be reduced (Regehr & Montevecchi 1997).

During the 2013 breeding season we recorded nocturnal predation of black-legged kittiwake chicks *Rissa tridactyla* by a peregrine falcon *Falco peregrinus* on Puffin Island, North Wales, UK (53° 19' 05" N, 04 °01 '40" W). The island is situated ~0.6km offshore and hosted approximately 385 breeding pairs of kittiwakes in 2013 (Natural Resources Wales, unpublished data).

As part of a wider study we deployed five time-lapse cameras (Ltl-Acorn 5210MC) throughout the kittiwake colony. One of these cameras was situated close enough to the breeding area to capture clear infra-red images which could identify night time/lowlight events. The camera was set to take one image every four minutes, 24 hours per day. Four active nests were in the field of view of the camera (Figure 5.1a).

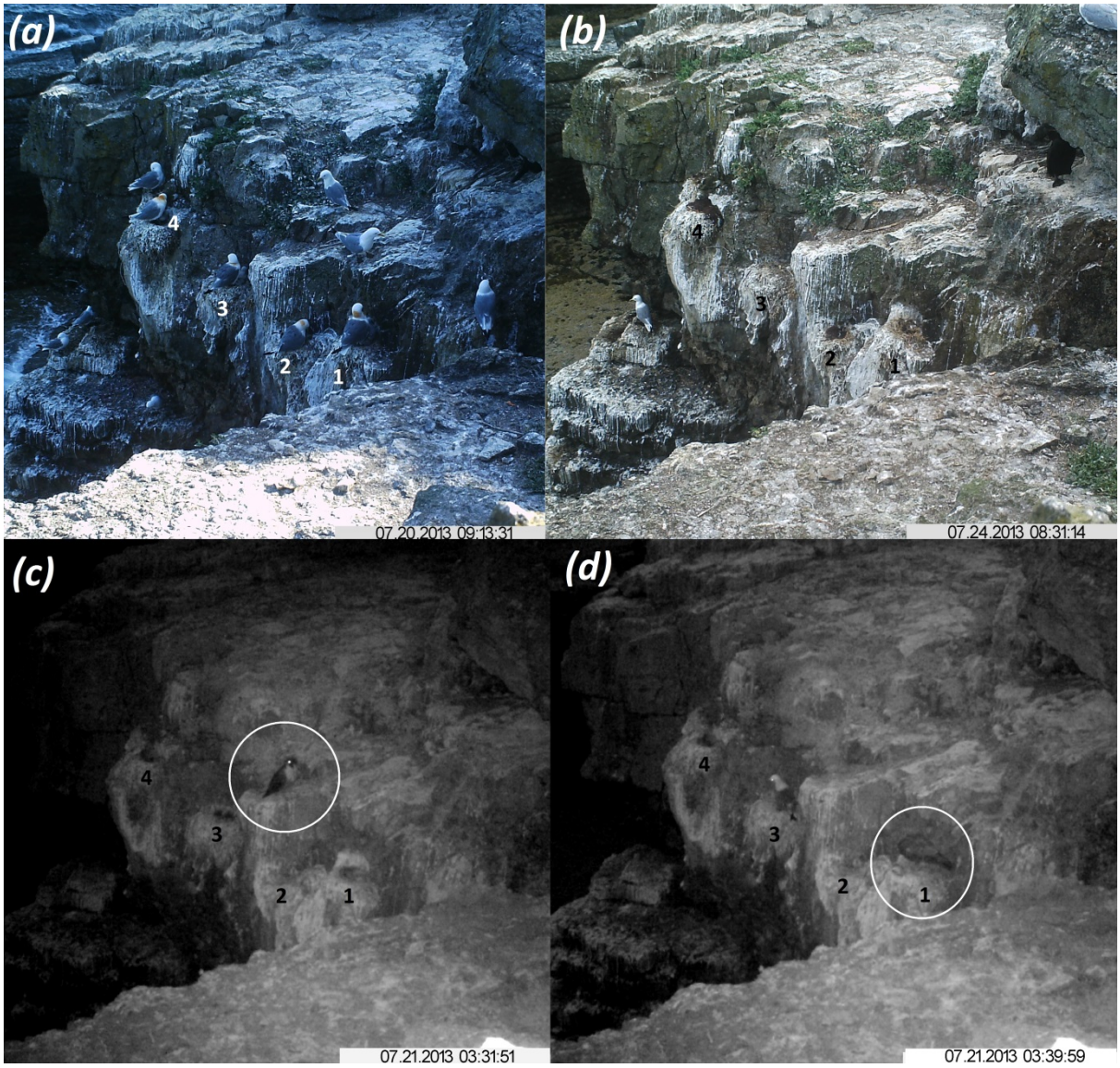

Figure 5.1 (a) The study plot 12 hours before the first predation event, all adults were on at least one chick, the four active nests are numbered. (b) The study plot one day after predation (24 July 2013), all previously active nests were empty, and the adults have abandoned the site. The bird present towards the left side of the image is not on an active nest. (c) The peregrine (circled in white) at the study site at 0331GMT on 21 July 2013 and shown eight minutes later (d) predating the chick at nest 1. Note the presence of an adult kittiwake at nest 3. This was the only adult to return when the Peregrine was present.

Between 20 July 2013 and 23 July 2013 all four nests in the field of view of the camera failed (Figure 5.1b). The failure was determined by images captured by the camera and further corroborated with human observations made on 26 July 2013. Up until 20 July 2013 these nests were at the chick rearing stage, with nests 1, 2 and 4 containing one chick and nest 3 containing two chicks. At the time of failure, chicks were aged between 4 and 16 days old. Inspection of the remote camera images identified a peregrine directly predating nests 1 and 3 (Figure. 5.1c-1d). The peregrine was observed directly predating nest 1 at 0327 GMT (21 July 2013) and nest 3 at 0337 (23 July 2013), 53 minutes, and 48 minutes before sunrise (0422 and 0425 respectively). The Peregrine stayed at nest 1 for between 12 and 16 minutes, and at nest 3 for between 16 and 20 minutes.

Predation was not directly observed at nests 2 and 4, however the behaviour of the adult kittiwakes and the sudden disappearance of chicks is indicative of predation. On 20 July 2013 at 2121 (sunset was at 2031) all four attending adults deserted their nests for between 32 and 36 minutes, the image taken at 2121 showed that as well as the adults, the chick in nest 2 was no longer present as it had been at 2117. On 21 July 2013 at 2110 (sunset was at 2029) this happened again at nest 4 with all adults leaving for 21-25 minutes, again the chick was no longer visible in the image taken at 2110, whereas it was visible in an image taken at 2106.

It would not have been completely dark during predation events, thus it is possible that the peregrine was using the low light conditions to enhance its chance of predation success. Hunting during a period of low light is likely to reduce the visual stimulus which would prompt mobbing behaviour of neighbouring birds (kittiwakes or large gulls) (Chandler & Rose 1988). It could also be that the consecutive nature of the predation events in the present case indicates the Peregrine remembered the location of the nest sites. Predation

by peregrines at night has been observed before, but only in the presence of artificial light, for example in the case of at a Balearic shearwater colony in Menorca (Wynn *et al.* 2010), or in cities where artificial light facilitates predation (Rejt 2004; DeCandido & Allen 2006). No predation events were recorded in the day time.

Kittiwake productivity in the UK has been declining in recent years (JNCC 2013). At Puffin Island during the 2013 field season productivity was notably low; a control plot of 62 apparently occupied nests failed to fledge a single chick. Nests at four other study sites on the island also all failed. A total of 9 nests (out of 9) in these other study sites failed while on chicks, but the remote cameras were not positioned close enough to record sufficient quality infra-red images. In addition to very low productivity, the timing of breeding was late. The average date of lying was on 13 June, whereas most Kittiwake eggs at colonies in the UK are laid by the end of May (Coulson 2011). This suggests certain other environmental parameters contributing to a poor breeding season. However by directly recording the peregrine predating nests on the island we can consider it as a contributing factor to breeding failure of the birds which did get to the chick rearing stage. The low numbers of chick rearing adult kittiwakes could have facilitated predation, with low adult density likely failing to provide strong enough deterrent to predators (Birkhead 1977, Gilchrist 1999).

Although predation of kittiwakes by peregrines has been observed before (Coulson 2011), and has even been speculated to be responsible for colony disappearance (Paine *et al.* 1990), the importance of such predation is largely unknown. Great skua *Stercorarius skua* and larger gull species are also known to predate kittiwake chicks, with the impact of such predation having before been considered (Furness 1981; Massaro *et al.* 2001)Furness 1981, Massaro et al. 2001). Such identification of causes of mortality allows decoupling of the

potential pressures acting upon populations. This not only allows us to quantify predation pressures, but also allows a more robust quantification of other drivers which may be acting upon a population.

While seabird predation by avian predators is widely accepted, we suggest that the use of remote cameras provides the possibility to identify and even quantify the occurrence of such events. Nest predation has been successfully recorded in other groups of birds (Cutler & Swann 1999), yet perhaps due to their often remote location seabird studies are lacking in this respect. In this study we have demonstrated this approach and have also captured images giving an insight into the behaviour of a top predator.

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Chapter 6

General discussion

General discussion

Movement plays a fundamental role in how most animals function in their environment. For mobile species, energy expended due to movement can account for a large proportion of daily energy expenditure (Brit-Friesen *et al.* 1989). Individuals able to manage their energy budgets so that energy expended does not overwhelm energy gained are more likely to have sufficient resources to invest in self-maintenance and reproduction (Nisbet *et al.* 2000; Ellison 2003). Recording animals using biologging devices allows continuous quantification of movement and can therefore provide insights into strategies animals may adopt to help them cope with the demands they face. This is especially the case for highly mobile species such as seabirds, which spend extensive periods of time out at sea; continuously observing such animals is impractical. The overall aim of this thesis was to reveal and examine the at-sea movement behaviours of a breeding seabird to develop an understanding of how individuals move during this period of their life-cycle. In particular, the potential consequences of movement on energy expenditure were examined. By instrumenting kittiwakes with accelerometers, we examined their time allocation to behaviours and how they interact with the wind conditions they face when flying to and from foraging areas. To achieve this we developed a user-friendly method for analysing the output of accelerometers in order to identify and quantify animal behaviour.

Key findings

During the analysis of accelerometer data from breeding kittiwakes on Puffin Island I was confronted with a range of methodological options for assigning behavioural classifications. Available approaches ranged from time-consuming and subjective approaches involving identifying behavioural patterns by eye (e.g. Gómez Laich *et al.* 2009), to potentially complex machine-learning approaches (e.g. Grünewälder *et al.* 2012). Furthermore, many

of the methods for classifying accelerometry data seemed to be limited in their applicability across studies and species. There is no doubt that the broad range of approaches have their uses and contribute to the growing number of insights provided by accelerometry studies of free-ranging animals. I concluded that there was an absence of a relatively simple method we could use to objectively assign behavioural classifications to our data. The method presented in **chapter 2** addresses this gap by providing a simple and objective approach for assigning coarse-scale behavioural classifications to accelerometry data. The method was developed to be applicable across species, as is evidenced using both humans and kittiwakes in the development and validation of the approach. By basing the technique on identifying breaks in readily calculable metrics of accelerometry, its implementation is straightforward and can be easily interpreted in relation to the behaviour of the instrumented animal.

The method we developed is suited to studies that need to identify coarse-scale behaviours. It is unlikely to be suitable for classifying fine-scale behaviours, however it could isolate periods of broader scale movement within which finer scale behaviours can be found. For example it can be used for identifying periods of flight, within which wing beat analysis can be applied (as in **chapter 4**). Ultimately the use of the method will be determined by the research questions being answered. By publishing this method in an open access journal along with the necessary R scripts to run the programme (Supplementary material S2.5), it is our intention that the method will not only be used, but will be enhanced over time as it is applied to a broader range of species displaying different behavioural profiles.

With the method for classifying acceleration data in place, in **chapter 3** we put it to use. The purpose of this study was to interrogate how kittiwakes breeding on Puffin Island

allocated their time to behaviour, and how such time-allocation affected energy expenditure. By collecting data on both incubating and chick-rearing birds, comparisons between these two periods of different energetic demands could be made. We demonstrated that the proportion of time kittiwakes spend flying has a substantial influence over the amount of energy they expend. We also demonstrated that chick-rearing kittiwakes spent a greater proportion of time flying than incubating kittiwakes, and that this results in a greater rate of daily energy expenditure for chick-rearing individuals. This difference in breeding stage time-allocation is generally assumed in seabird studies, however we provided direct empirical evidence for it in this study. In **chapter 3**, we also found evidence for behavioural compensation, whereby kittiwakes limited the proportion of time they spent flying per day, and also as duration of foraging trip increased. This finding not only provides support for the idea of an energetic ceiling, whereby individuals are constrained in their total daily energy expenditure (Welcker *et al.* 2010), but also highlights the potential importance of allocation of time to behaviour in avoiding this energetic ceiling. This finding also resulted in a methodological consideration. As we found a lack of a proportional relationship between time away from the colony and rate of energy expenditure, we suggest that considering time away from the colony alone as an indication of energy expenditure is not sufficient for kittiwakes, or indeed other seabirds.

Having identified the energetic influence of flight in **chapter 3**, in **chapter 4**, we examined this behaviour in greater detail, specifically in breeding individuals. The basis of this chapter was a dataset consisting of both GPS and accelerometry data collected on kittiwakes breeding on Middleton Island, Alaska. By identifying periods of flight from accelerometry data using the method developed in **chapter 2**, we then examined these data in combination with GPS and wind data to investigate the influence of windscapes on the flight behaviour of kittiwakes. One of the potential pitfalls of plotting animal movement on

a 2-dimensional map is that it is easy to forget that the animals being studied are moving through a dynamic environment. By analysing movement in relation to wind speed and direction, we address this pitfall. The work in **chapter 4** highlighted that wind conditions did not seem to have an influence on the initiation, course, or destination of commuting flights when kittiwakes were away from their nests on foraging trips. Consistency in flight direction and destination, regardless of wind speed and direction, indicated that over the study period, prey location was likely to be the most important factor influencing the commuting flights of kittiwakes. Wind conditions did however influence the speeds that kittiwake flew, both in terms of their absolute ground speed (speed as it would be measured from a map) and their air speed (the speed at which they flew once the influence of wind was removed). These findings suggest that kittiwakes compensate for wind speeds when in flight by adjusting flight speeds towards a maximal range speed - a speed that minimises energy expended per unit travelled. By measuring wing beat parameters it became apparent that rather than increase the frequency at which they flap, kittiwakes increased the strength with which they flapped their wings in order to fly faster.

Chapter 4 examines the flight behaviour of kittiwakes in greater detail than any previous study. Considering that wind speeds tend to be far greater at sea than on land, and seabirds often fly great distances both during and outside of the breeding period, understanding the influence of wind on the movement patterns of seabirds is imperative. Studies focusing on flight behaviour of seabirds tend towards larger birds, and as such, much work has been done on the flight behaviour of the albatrosses and some on species such as cormorants and shags (e.g. Yoda *et al.* 2012; Kogure *et al.* 2016). By uncovering the influence of wind conditions on kittiwakes, we have contributed to the limited understanding of the influence of wind on these seabirds. Our findings could also be applicable to other seabirds that employ a similar style of flight to kittiwakes. Considering

this study in a broader framework, our findings highlight the importance of considering trade-offs between influential extrinsic factors (in this instance wind and probable prey location) when examining movement.

The final chapter, **chapter 5,** documents the predation of kittiwake chicks by a peregrine falcon. Considered alone, the contribution of this piece of work is two-fold. Primarily it is an observation of predatory behaviour by a peregrine falcon on kittiwake chicks during pre-dawn hours - behaviour that has not been presented in the literature before. Secondly, the work highlights the value of using remote cameras to monitor seabird nests. Remote cameras have been shown to be valuable for monitoring seabird productivity (Lorentzen *et al.* 2011), and through increasing the frequency at which photos are taken we have demonstrated their value for capturing short-lived events such as predation. By considering this observation in context of the other studies presented in this thesis, this study highlights that although energy optimisation in movement may be important to individuals, other sweeping factors such as predation can ultimately override their importance. The observation also serves as a reminder that such animals are operating in complex environments where multiple extrinsic and intrinsic factors shape the fate of individuals.

Implications, considerations and future directions

As seabirds are a highly threatened group of species (Croxall *et al.* 2012), which for a large proportion of their time operate away from the land, understanding their movement patterns is integral for developing a more in-depth understanding of their ecology and conservation requirements. This thesis has not focused on the application of the findings to conservation; however, through gaining key insights into kittiwake movement throughout their breeding period, findings presented may help to inform future conservation decisions. Regardless of this, we have provided novel insights into the daily lives of kittiwakes. The

findings presented have implications for other seabirds, and indeed other animals. This is especially true in terms of trade-offs that individuals might make to manage their energy expenditure when providing for young and/or commuting to foraging sites. Indeed, by measuring the movement ecology and energetics of seabirds in such a way, mechanistic links underpinning why some seabirds fail can be identified (e.g. Ponchon *et al.* 2015).

There are, of course, limitations to the biologging approach we employed that need to be considered. Notably the deployment of all tracking devices likely impacts the behaviour of the individual carrying the device, be it through the added weight of the device (Vandenabeele *et al.* 2012), device attachment impacting the hydro or aerodynamic profile of the animal (Vandenabeele *et al.* 2014), or investigator handling of the animal having a detrimental impact (Carey 2011). Continued miniaturisation of devices and a greater understanding and consideration of the impacts these devices have (Passos *et al.* 2010; Vandenabeele *et al.* 2012, 2014; White *et al.* 2013) are helping to reduce these impacts. Within each chapter we have noted, where appropriate, the potential limitations accrued from biologger devices. This may mean that absolute values presented in each of the relevant chapters (**chapters 4 and 5**) could have been impacted by logger attachment, however the overall findings are probably not unduly influenced by such effects.

As well as providing insights into the movement ecology of breeding seabirds, the findings presented here highlight areas to explore in future studies. For example, it is likely that the adults whose chicks were predated in **chapter 5** would have subsequently behaved differently than they would have if they were required to continue providing for their young (as per the birds in **chapters 2 & 3**). Without the constraints of having to raise young, their movement patterns could have been very different (Votier *et al.* 2011). Unfortunately we were not able to deploy or retrieve biologgers on such birds. Spatial segregation in

successful versus unsuccessful albatrosses has been recorded (Clay *et al.* 2016), however energetics/behaviour focused studies are lacking and could contribute to developing a more in-depth understanding of the trade-offs individuals make when confined to central place foraging. It may be that the difference in movements may not be so stark in colonies that tend to be more successful, thus indicating sufficient readily available resources. Quantifying prey resources near the colony also represents another possible future direction of study. By having confidence in the distribution of prey, the factors determining seabird movements as presented in **chapter 4** could be verifiable (Suryan *et al.* 2002). Furthermore, quantifying prey intake would allow for a more complete understanding of how energy budgets of individuals are balanced, as opposed to just using energy expenditure as an indication of how an individual is optimising behaviour. Quantification of prey intake has been achieved through biologging tools before (Sato *et al.* 2008; Carroll *et al.* 2014), however in combination with fine scale flight behavioural data, such as that presented in **chapter 4,** it could allow for a far greater interrogation of foraging decisions in relation to balancing energy budgets, as opposed to just optimising energy expenditure alone.

Conclusions

This thesis has contributed a method for the analysis of accelerometry data and has used this method to examine some key aspects of the movement ecology of kittiwakes. By identifying how kittiwakes allocate their time when at sea, we subsequently managed to quantify the associated energy expenditure of variation in time allocation, providing evidence for behavioural compensation. With our findings highlighting the overwhelming energetic importance of flight, we further investigated the flight behaviour of kittiwakes. We identified the overriding importance that wind conditions play in commuting flight

distributions, while uncovering the plasticity individual can employ in their flight behaviour in order to reduce the potential energetic impacts of wind conditions. Furthermore, we have detailed previously undocumented behaviour of an avian predator and provided justification for the use of remote cameras. The work we present focuses on one species, however our findings have been framed in a wider biological context and should therefore be applied to, considered in, or tested on, other species.

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